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ERRATA AND AUTHOR'S EMENDATIONS

Page 70, line 7, "*U. hordei*" should be "*U. nuda*."
Page 72, eleventh line from bottom, add "a component of gluten" after "prolamin."
Page 73, line 24, "conidia" should be "sporidia."
Page 73, seventeenth line from bottom, "conidia" should be "sporidia."
Page 80, second line from bottom should read "salts in plant materials, also globulins."
Page 142, Figure 7, the 1.5 mm. bar under "Fruits 2½ to 2¾ inches in diameter" should be 0.7 mm. high instead of 0.9 mm.
Page 166, line 12, "240 μ" should be "240 mμ."
Page 166, line 13, "365 μ" should be "365 mμ."
Page 166, line 20, "365 μ" should be "365 mμ."
Page 166, line 24, "313 μ" should be "313 mμ."
Page 166, line 29, "240 μ" should be "240 mμ."
Page 169, sixteenth line from bottom, "can" should be "can not."
Page 185, line 12, omit "when necessary."
Page 186, Table 2, insert figures 1 and 3 under heading "Experiment No."
Page 191, line 18, insert "and waxy" after "nonwaxy."
Page 223, Table 2, "Diameter" in boxheads of third to sixth columns, inclusive, should be "Length."
Page 234, seventeenth line from bottom, "decreasing number of additional seedlings" should be "slowly increasing number of seedlings."
Page 236, Table 3, in boxheads for columns three to seven and last column, "diameter" should be "height."
Page 236, Table 3, column nine, insert "Number."
Page 236, last sentence, first paragraph, "the remaining trees" refers to the 20–40 per cent which fall in the 1-inch height class.
Page 247, seventeenth line from bottom, "6.4" should be "0.4."
Page 390, Table 4, second column, insert "retained" after "buds."
Page 451, Table 2, dry weight for leaf and top stem for March 27 analyses should be "10.0" and "0.5," respectively.
Page 454, Table 9, first column, "July 13" should be "July 12."
Page 455, Table 10, first column, "Aug. 22" should be "June 22."
Page 455, Table 11, first column, "June 27" should be "June 22."
Page 455, Table 12, first column, "June 27" should be "June 22."
Page 455, Table 12, first column, "July 12" should be "July 13."
Page 455, Table 12, third column, lines 5 and 6, "Top leaf" and "Base leaf" should be "Top stem" and "Base stem," respectively.
Page 566, tenth line from bottom, "actions" should be "cations."
Page 648, fourth line from bottom, the first "It" should be "If."

JOURNAL OF AGRICULTURAL RESEARCH

VOL. 38 WASHINGTON, D. C., JANUARY 1, 1929 No. 1

A BACTERIAL STRIPE DISEASE OF SORGHUM[1]

By CHARLOTTE ELLIOTT, *Associate Pathologist, Pathological Laboratory* and *Office of Cereal Crops and Diseases*, and ERWIN F. SMITH,[2] formerly *Senior Pathologist in Charge, Pathological Laboratory, Bureau of Plant Industry, United States Department of Agriculture*

INTRODUCTION

Bacterial diseases of broomcorn and other sorghums (*Holcus sorghum* L.) causing reddening of the tissues have been attributed to several distinct organisms (*3, 5, 16, 17, 26, 27*),[3] and in some instances the organisms were isolated and named without proof of their pathogenicity. Some early descriptions of organisms were meager and unsatisfactory, and in most cases the descriptions of lesions do not define sufficiently clearly the type of red spotting caused by a particular organism. The natural result has been considerable confusion as to what types of red spotting on sorghum are caused by bacteria and which organisms are to be considered true pathogenes. A review of these earlier papers, a discussion of the causal organisms named in them, and the relationships of these organisms to *Bacterium andropogoni* E. F. Smith, will be found under the heading "Comparison with similar diseases." The work on *Bact. andropogoni* reported in this paper was undertaken to complete the description of this organism, and to define as clearly as possible the symptoms and character of the disease caused by it.

PREVIOUS WORK WITH BACTERIUM ANDROPOGONI

In 1905, one of the writers (*27*) published a photograph of broomcorn leaves showing lesions of a bacterial disease produced by inoculation in the greenhouse. These lesions were described as stomatal infections causing elongating red or red-brown stripes on a green background. The under surfaces of the diseased areas were covered by red crusts, the dried bacterial ooze from the interior of the leaves.

In the same year Smith and Hedges (*28*) published an article entitled "Burrill's Bacterial Disease of Broom Corn." No illustrations were given, but the symptoms of the disease were the same elongating red-brown blotches, which readily fused and caused the death of many large leaves. Red crusts on the under surfaces of the lesions were also characteristic. The disease was reproduced by spraying with pure cultures of the organism obtained from these

[1] Received for publication June 21, 1928; issued January, 1929. This is an extension of the paper presented by the writers at the 1924 meeting of the American Phytopathological Society (*18*), supplemented by reference to an earlier manuscript by the late Erwin F. Smith covering a review of the early literature and the investigations conducted by him and his assistants from 1904 to 1908. Reference is made wherever material from this earlier manuscript is used. All color and photographic work was done by J. F. Brewer.

[2] Died Apr. 6, 1927.

[3] Reference is made by number (italic) to "Literature cited," p. 21.

lesions, and the organism was reisolated. No name was given the organism, but from the title of the paper it may be assumed that the writers believed the disease to be the same as Burrill's disease, but did not consider the organism to be that described by him (*5*) and by Kellerman and Swingle (*15*). It was described as nonsporiferous, motile, aerobic, white, and sticky on agar. It blued litmus milk and finally rendered it gelatinous, did not liquefy gelatin, did not reduce nitrates, produced little if any indol, had little diastasic action on potato starch, and had a thermal death point of 47° C.

In 1911 Smith (*27*) again mentioned the spot disease of sorghum and broomcorn, stating that he had reproduced the disease with pure cultures of an organism that was not *Bacillus sorghi* Burrill, and showed two good figures of early stomatal infections. He described the organism as nonsporiferous, with 1 to 3 polar flagella, white on culture media, aerobic, nonliquefying, and nonreducing (nitrates). He named the organism *Bacterium andropogoni*, n. sp. This was the same organism with which he had done his earlier work, and the descriptions of lesions agree in all three instances. These three published accounts of the disease constitute a summary of the work done by Smith and his assistants from 1904 to 1908. This work was recorded in greater detail in an unpublished manuscript, in which he stated that the disease was observed only on broomcorn and sweet sorghums and that he studied it only in the District of Columbia and knew nothing further of its distribution. The recent work reported in this paper is a continuation of that already reported on *Bact. andropogoni*.

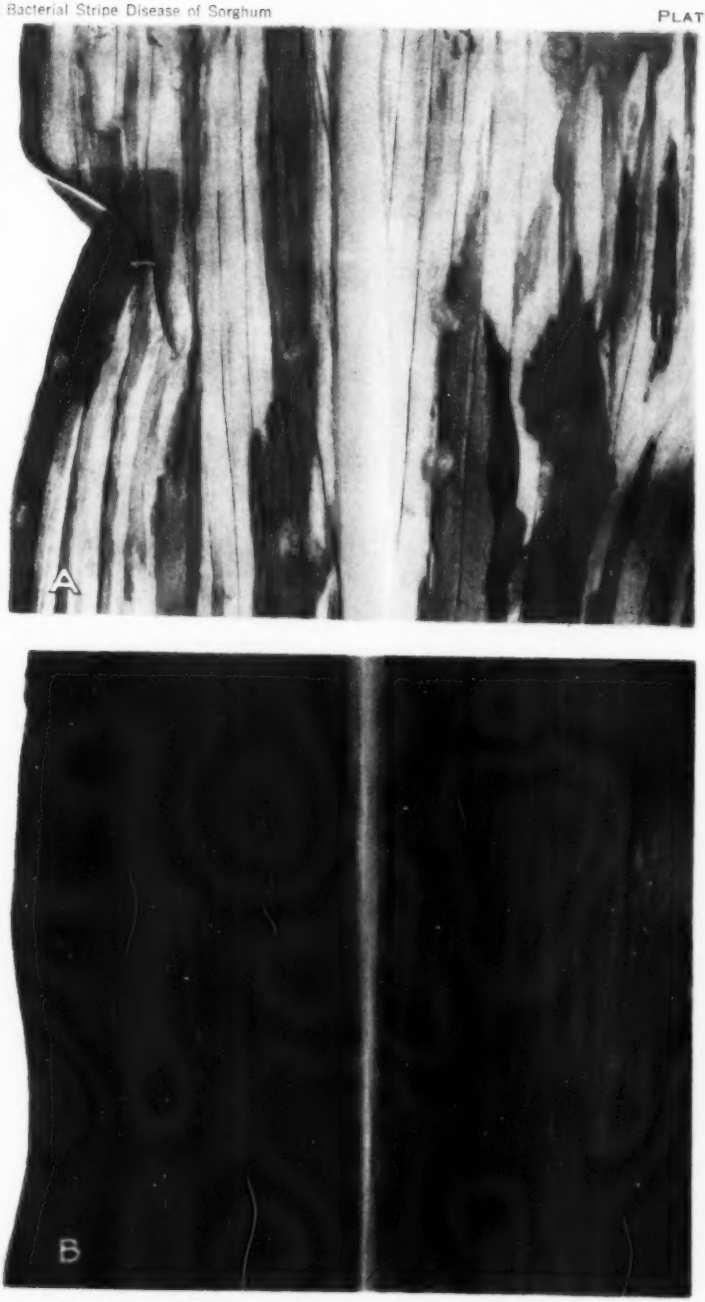
DESCRIPTION OF LESIONS

During the summers of 1922 and 1924 red leaf lesions, similar to those described and figured by Smith (*27*) and by Smith and Hedges (*28*), were collected on sorgos, grain sorghums, grass sorghums, and broomcorn at the Arlington Experiment Farm, Rosslyn, Va., and at Manhattan and Hays, Kans. The leaves were streaked with elongating red blotches ranging in length from a few millimeters to many centimeters. The lesions were either narrow and bounded by veins or were fused and covered a large part of the leaf surface. The ends of lesions were either blunt or extended into long jagged points. The red color was never marginal but was continuous throughout the lesion, and the red crusts of dried bacterial exudate on the lower surfaces were very characteristic. From older lesions this exudate may have been washed away by rains. These bacterial lesions are most abundant on the leaves but may extend from the leaves to the sheaths and stalks. The symptoms from both natural and artificial infections on various hosts are illustrated in Plates 1 to 8, inclusive.

Red discolorations on leaves, sheaths, stalks, and heads of many varieties of sorghum are host reactions to injuries of various kinds (mechanical, insect, fungous, or bacterial), the color reaction depending chiefly upon the variety injured. The form of the lesion is determined by the cause of the injury.

The bacterial lesions produced by *Bacterium andropogoni* on all the varieties of sorghum are the same in form, namely, elongating red streaks and blotches, but the color of the lesions varies from a brick red (pl. 2, B) to dark purplish red (pl. 1), depending on the variety attacked. The same organism produces very dark purplish red lesions on Silvertop, Sugar Drip, Early Amber, chicken corn,

Natural infection on sorghum (S. P. I. No. 54538, Java) with *Bacterium andropogoni* Arlington Experiment Farm, Rosslyn, Va., September 5, 1922. X 1.



A.—Natural infection on sorghum (S. P. I. No. 51976, Rejaf, Sudan) with *Bacterium andropogoni*, at Arlington Experiment Farm, Rosslyn, Va., September, 5, 1922. Note yellow-brown lesions and exudate scales. X 1.

B.—Infection on sorghum (S. P. I. No. 51977, Rejaf, Sudan) three weeks after inoculation with *Bacterium andropogoni* (isolation No. 13) at Arlington Experiment Farm, Rosslyn, Va., September 13, 1922. X 1.

and Sudan grass, and light brick-red lesions on Red Amber and S. P. I. No. 51977. On kafir (S. P. I. No. 51611) the reaction is more of an intermediate brownish red.

There also are certain varieties of sorghum, such as S. P. I. Nos. 51976 and 51978 and shallu Agrostology No. 2650, that show no red reaction to injury. Bacterial lesions on these plants vary from light to dark brown and the crusts of exudate are yellowish brown. (Pls. 2, A; 4, A; and 6, A.)

ISOLATIONS AND INOCULATIONS

As *Bacterium andropogoni* is slow growing and sensitive to sterilization with mercuric chloride, all but the first few isolations were made after the tissue had been washed through 12 sterile water blanks. With careful washing pure cultures of the organism may be obtained in this way. Of 30 or more isolations from typical red lesions on leaves, all but the first 2 produced practically pure cultures of *Bacterium andropogoni*. Of 4 isolations from red streaks on stem and sheath, 1 produced a pure culture of the organism. The results of two sets of isolations from red spots on seed, after treating them with mercuric chloride for two minutes, were negative.

Four isolations from yellowish brown lesions (pls. 2, A, and 6, A) occurring on plants that showed no red reaction produced pure cultures of the same organism as that isolated from the red lesions. All isolations made from various kinds of sorgo, grain sorghum, broomcorn, and grass sorghum produced colonies of the same organism. The colonies begin to appear after 48 hours as tiny translucent points or dots, which in three or four days increase to white colonies 1 to 2 mm. in diameter. Colonies later may grow to 4 or 5 or even 7 mm. (Pl. 9, E.) The pathogenicity of nine of these isolations, including those from both leaf and sheath and from both red and yellow lesions, was proved by repeated inoculations and reisolations.

Inoculations were made in both the field and the greenhouse by spraying with water suspensions from young agar cultures. Some of the plants were wounded before spraying, but when conditions are favorable infection occurs just as readily through uninjured as through injured tissue. Infection depends so much upon environmental conditions of temperature, and especially of moisture, that only about half of the 60 to 70 inoculations gave positive results. In the field, warm cloudy days following precipitation are most favorable for the spread of the disease, and in the greenhouse damp chambers must be used to keep the atmosphere about the plants saturated or nearly saturated with moisture to be certain of securing infections.

The 30 or more successful inoculations, however, gave ample proof of the pathogenicity of the organism. (Pls. 2, B; 5, A; 5, B; 6, A; and 6, C.) In some cases only small, scattered lesions developed, while in others the lesions spread over a large part of the inoculated leaf surface. Cultures isolated from red lesions produced red lesions (pl. 5, A) on varieties showing a red reaction and yellowish brown lesions on plants showing that reaction. Cultures isolated from yellowish brown lesions produced red lesions (pl. 5, B) on plants of that reaction and yellow-brown lesions (pl. 6, A) on plants that showed no reddening. From this it is apparent that the causal

organism is the same for the two types of lesion, the difference in color being due to a difference in host reaction.

CAUSAL ORGANISM

The cultures used almost exclusively for morphological, cultural, and physiological studies were isolated from typical leaf lesions as follows: No. 8 from red lesions on sorgo (S. P. I. No. 54538), August 1, 1922; Nos. 9 and 32 from yellow lesions on sorghum (S. P. I. No. 51976), August 23, 1922, and August 17, 1923, respectively; and No. 33 from red lesions on Dwarf broomcorn (C. I. 442), August 17, 1923. Cultures Nos. 8 and 9 were used during the season of 1922–23 and cultures Nos. 32 and 33 during that of 1923–24. Unless otherwise stated, tests were made at room temperature, about 23° C.

MORPHOLOGY

Bacterium andropogoni is a short rod with rounded ends, arranged singly or in pairs.

Smears made from 24-hour beef-peptone agar slants (pl. 9, F) and stained with gentian violet vary from 1.3 to 2.5 μ in length and 0.4 to 0.8 μ in width with an average of 0.64 by 1.76 μ.

Capsules (pl. 9, D) are present on beef-peptone agar. Spores or endospores are not formed. On beef-peptone agar the bacteria are motile, having one to several bipolar flagella. (Pl. 9, C.)

The organism is Gram-negative, not acid-fast, and stains readily with gentian violet and carbol fuchsin and less readily with methylene blue.

CULTURAL CHARACTERS

BEEF-PEPTONE AGAR COLONIES.—On beef-peptone agar (about pH 6.8) colonies of *Bacterium andropogoni* grow slowly. After 48 hours they appear as small points and dots and in 4 to 5 days are 2 to 3 mm. in diameter. They are round, smooth, glistening, slightly raised, with entire margins. (Pl. 9, E.) By reflected light they are white, but by transmitted light their centers are denser and of a very light tan color with thin bluish borders. (Pl. 9, G, H.) As the colonies become older the distinction between center and margin is less marked. While the colonies are young they are soft and very viscid, so that the whole colony comes up from the agar when an attempt is made to remove a part with the needle. Internally the colonies are finely granular with occasional traces of concentric cross-hatching. (Pl. 9, I.) Embedded colonies are at first lenticular, but in a few days they become spherical with irregular margins.

About the colonies when they are 1 to 2 weeks old, clear circles 1 to 2 mm. wide begin to appear in the agar. Around these clear areas the agar is clouded, forming a halo 2 to 4 mm. broad, fading at the outer margin into the usual appearance of the agar. When the colonies are 3 to 4 weeks old the clear areas and halos are less distinct. (Pl. 9, A.) These halos were recorded by Smith as occurring in agar plates in 1905.

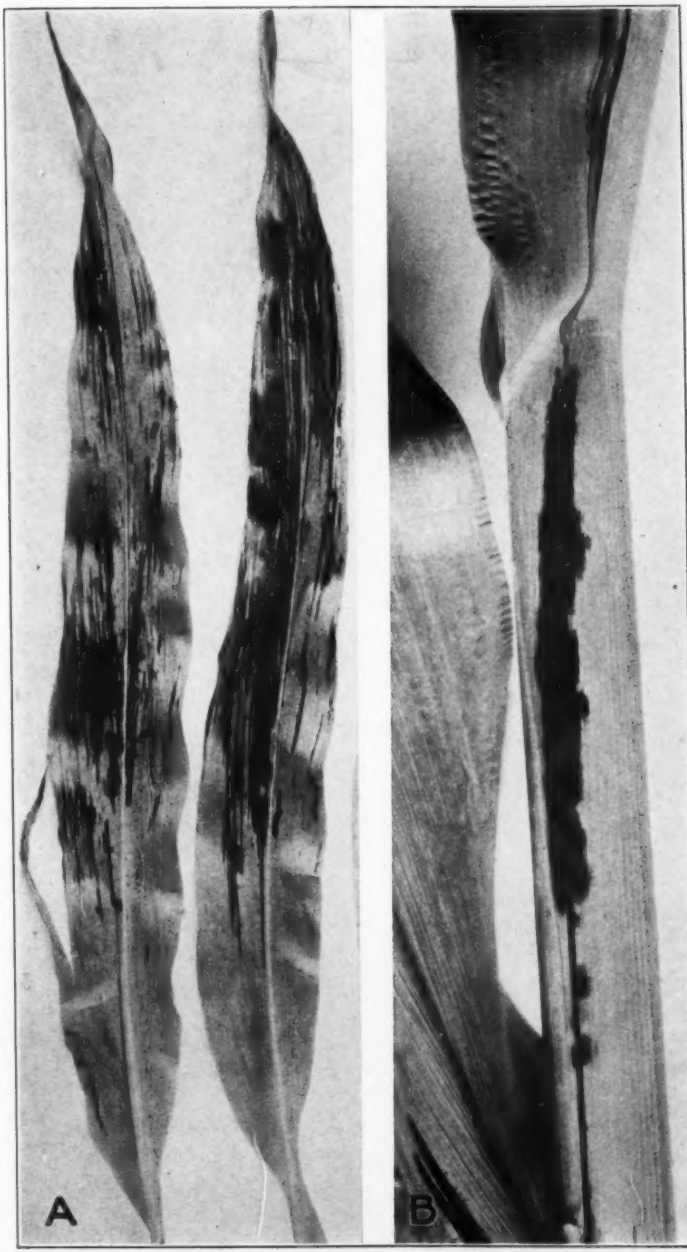
BEEF-PEPTONE AGAR SLANTS.—There is slight growth in 24 hours. After 48 hours the growth is moderate, filiform, sometimes raised, glistening, smooth contoured, white, viscid, with a slight odor of decay. In two weeks the agar clears along the margin of the streak and clouds outside the clear area.

POTATO-DEXTROSE AGAR COLONIES.—Colonies grow slowly, beginning to appear in 48 hours. After three days they are 1 to 2 mm. in diameter, and the agar about them is clouded for a distance of 2 to 3 mm. Five-day colonies are 2 to 4 mm. in diameter, and the clouding in the agar has disappeared. The colonies are raised, smooth, glistening, and white. They do not have sharply marked-off centers and margins as on beef agar. The centers, which are rubbery and easily lifted from

EXPLANATORY LEGEND FOR PLATE 3

A.—Dark-red lesions on sorghum (S. P. I. No. 51976, Rejaf, Sudan) from natural infection by *Bacterium andropogoni*, collected at Arlington Experiment Farm, Rosslyn, Va., August 30, 1922. × ½.

B.—Red sheath lesions on sorghum (S. P. I. No. 51977, Rejaf, Sudan) from natural infections by *Bacterium andropogoni*, collected at Arlington Experiment Farm, Rosslyn, Va., August 23, 1922.



(For explanatory legend see page 4)

(For explanatory legend see page 5)

the agar, are cream colored by transmitted light and not so dark as on beef agar. The margin or newer growth is only slightly viscid. The colonies are finely granular. In very young colonies there are sometimes traces of fish-scale markings. Colonies grow larger on potato dextrose than on beef agar. Colonies 2 weeks old may be 1 cm. or more in diameter and are butyrous in consistency. Only traces of viscidity remain.

POTATO-DEXTROSE AGAR SLANTS.—There is just a trace of growth after 24 hours. After five days growth is abundant, spreading, smooth, white, and glistening, and the precipitate at the base of the slant is cream colored. The consistency is viscid. There is no odor. At the end of two weeks there still is no odor, but the consistency is butyrous.

GELATIN PLATES.—Growth is slow, colonies beginning to appear after 48 hours. In three to four days colonies are 1 to 3 mm. in diameter. The center is small, raised, capitate, smooth and shining, and surrounded by a broad thin border contoured on the surface, with an undulate margin. At the end of about a week colonies are 6 to 7 mm. in diameter. (Pl. 9, B.) The center has flattened out somewhat, but other characteristics are as stated above. There is no evidence of liquefaction at any time. When colonies are about 3 weeks old there is a narrow clear ring about each one with a broad denser margin or halo as on beef agar. Colonies at this time are 1 cm. in diameter.

LOEFFLER'S SOLIDIFIED BLOOD SERUM.—Growth after six weeks is moderate, filiform, white, glistening to dull, and somewhat contoured. There is no evidence of liquefaction.

GELATIN STABS.—Gelatin stabs were placed in the incubator at about 18° C. There was good growth after two to three days, but even after nearly two months there was no evidence of liquefaction. On the same media and at the same temperature other organisms slowly liquefied the gelatin.

POTATO CYLINDERS.—At the end of a month growth is moderate, filiform, flat, glistening, smooth, and viscid. The medium becomes gray. Tested with Lugol's iodine solution, the checks produced a deep-blue color, while inoculated cylinders turned reddish blue, indicating a weak diastasic action.

BEEF-PEPTONE BOUILLON.—Growth is slow. There is light clouding in 24 hours, and moderate clouding in 48 hours. In 3 to 4 days a ring forms at the surface, which may grow out into a thin lacelike pellicle, readily falling when shaken. Growth is best at 22° to 30° C. A fine granular surface growth occurs in 24 hours and a moderate to heavy clouding in 4 to 5 days. The precipitate is viscid.

COHN'S SOLUTION.—The organism produces only a trace of clouding during the first few days. This may disappear later so that an observation made three weeks after inoculation would record no growth.

USCHINSKY'S SOLUTION.—There is a heavy white clouding at the end of a week and a thin pellicle with fine reticulate markings or a lacelike pattern. After two weeks the pellicle may become heavy. Pellicle and precipitate are viscid. There are a few small crystals.

FERMI'S SOLUTION.—Clouding is light, with a thin pellicle, which readily falls. There is little or no precipitate.

PHYSIOLOGY

TEMPERATURE RELATIONS.—The optimum temperatures for growth in beef-peptone bouillon are between 22° and 30° C. Growth is lighter and slower as temperatures decrease below 20°. At 5° to 6° there is only a trace of clouding after two weeks. No growth was observed at 1.5°, but tubes transferred from this to room temperature became clouded, showing that the organism remained alive at that temperature. The maximum temperature for growth is between 37° and 38°. The thermal death point is 48°.

CHROMOGENESIS.—Growth is white by reflected light on all media. By transmitted light on agar the denser central portion is cream to light tan.

OPTIMUM REACTION AND TOLERATION LIMITS.—The optimum reaction for growth in beef-peptone bouillon is Fuller's scale +17 to +21 (pH 6.6 to pH 6.0). There was slight growth at −2 (pH 8.3) and no growth at − 3 (pH 8.6). There was growth at +30 (pH 5.2) after 10 days, but no growth at +31 (pH 5.0).

EXPLANATORY LEGEND FOR PLATE 4

Natural infections on leaves of two different plants of sorghum (S. P. I. No. 51976, Rejaf, Sudan), at Arlington Experiment Farm, Rosslyn, Va., August 23, 1922. × 1

A.—Lesions light yellowish green to brown.
B.—Typical deep-red lesions.

TOLERATION OF ACIDS.—There was good growth in 0.1 and 0.2 per cent tartaric, malic, and citric acids in neutral bouillon with ranges from pH 7.2 to pH 5.8.

Malic, tartaric, and citric acids were also added to neutral broth to give definite pH reactions. Growth occurred in tartaric at +34 (pH 5.0), but not at +38 (pH 4.8); in malic at +38 (pH 5.0), but not at +40 (pH 4.9); in citric at +38 (pH 5.2), but not at +40 (pH 5.0).

INDOL PRODUCTION.—Indol is not produced. Tests were made with sulphuric acid and sodium nitrite on beef-peptone broth cultures and on cultures in 1 per cent peptone solutions containing 0.5 per cent disodium phosphate and 0.1 per cent magnesium sulphate.

HYDROGEN SULPHIDE PRODUCTION.—Hydrogen sulphide is not produced. Tests were made in lead-acetate agar as recommended in the Manual of Methods (*29*) and in beef-peptone broth and agar and potato cylinders with suspended strips of lead-acetate paper.

RELATION TO OXYGEN.—There was no clouding in the closed arms of fermentation tubes in peptone water containing 2 per cent maltose, saccharose, dextrose, mannit, lactose, or glycerin. In agar shake cultures containing the same sugars, colonies grew to the depth of 1 cm. below the surface in maltose and lactose, but to only half that depth with other sugars. The organism is aerobic.

DIASTASIC ACTION.—On beef-extract and beef-infusion agar plus 0.2 per cent starch, there is at the end of a week a definite partially cleared zone, 2 to 3 mm. wide, shading into the blue of the surrounding medium when treated with iodine. There is no entirely clear area, indicating that the starch is only partially hydrolyzed.

MILK.—No acid or rennet curd is formed. Peptonization begins to be evident after about a week, but progresses very slowly. The color becomes a deeper cream than the check. After about three months the milk may become gelatinous in consistency, but the medium may remain liquid until it dries down.

REDUCTION OF LITMUS MILK.—Lavender-colored litmus milk turns blue in 4 to 5 days, and reduction begins at the bottom of the tubes in about 10 days. The litmus may be entirely reduced in three weeks, although complete reduction often takes longer. After six months one set of tubes of litmus milk had become "light celandine green" (*25*). Litmus milk seems to become gelatinous more generally than plain milk after three months.

REDUCTION OF METHYLENE BLUE.—Methylene blue in milk begins to lose color after two to three weeks and is completely reduced after about one month.

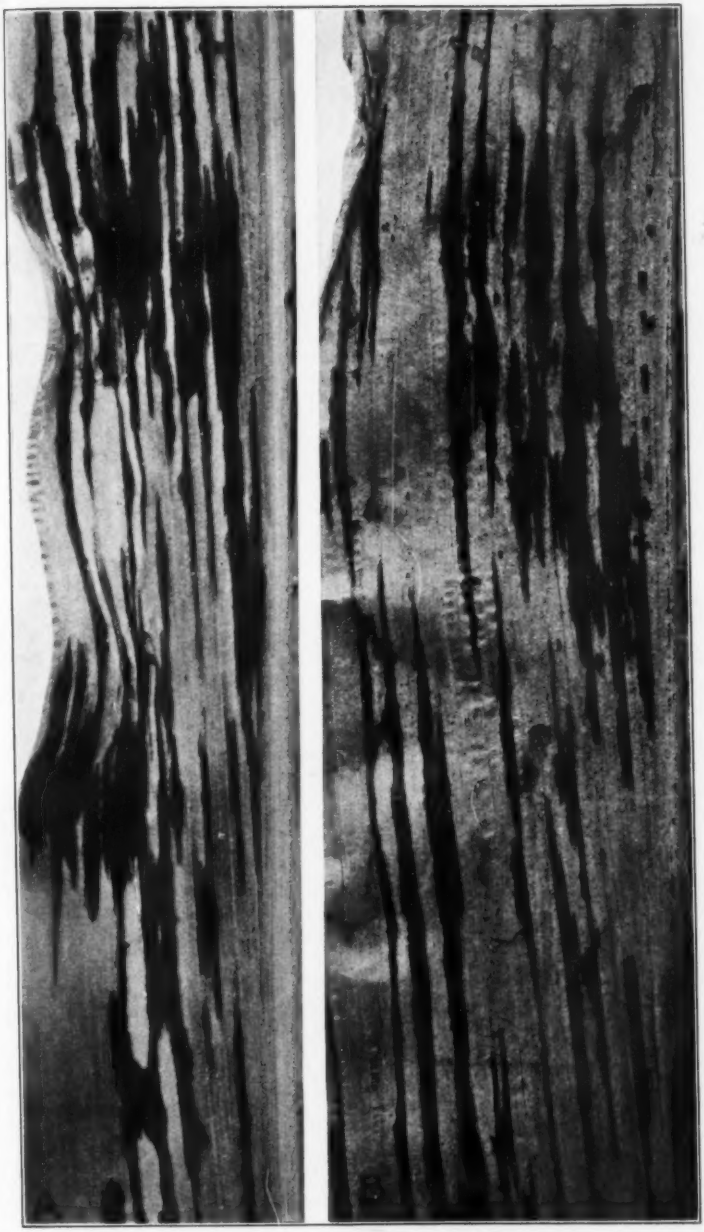
NITRATE REDUCTION.—Cultures were grown in nitrate-peptone broth, peptone broth, synthetic liquid nitrate medium, and peptone agar with 2 p.p. m. potassium nitrite. In two tests in nitrate-bouillon cultures with potassium iodide (1: 250), starch water, and sulphuric acid, there was no evidence of nitrate reduction. Tests with sulphuric acid and α-naphthylamine as recommended in Manual of Methods (*29*) also gave negative results. Nitrate-peptone broth and peptone-broth cultures tested with Nessler's reagent for ammonia showed positive reactions. The synthetic nitrate medium showed a negative test for ammonia and also for nitrites. Tests for nitrites in peptone-agar plus 2 p. p. m. potassium nitrite were positive. Tests were made on the third, seventh, and seventeenth days. This organism does not reduce nitrates.

FERMENTATION TESTS.—Tests were made in media containing peptone and the carbon compounds listed in Table 1. No gas was produced from any medium, and acid was produced from only dextrose, xylose, and arabinose. With all the substances tested except arabinose, the reactions begin to show alkalinity in 2 to 3 days, in the earlier tests attaining a maximum alkaline reaction in about 10 days—saccharose, 7.3; dextrose, 6.8; lactose, 7.2; maltose, 7.2; glycerin, 7.0; mannit, 7.2; and raffinose, 7.6—and in later tests showing increasing alkaline reaction through several weeks. In two weeks there is a decided rise in hydrogen-ion concentration in dextrose, xylose, and arabinose, but not in the other carbon

EXPLANATORY LEGEND FOR PLATE 5

A.—Red lesions on sorgo (S. P. I. No. 54538, Java) 13 days after spraying with a water suspension of *Bacterium andropogoni* (isolation No. 8, from red lesions on same strain of sorgo), Arlington Experiment Farm, Rosslyn, Va., collected and photographed August 30, 1922. × 1.

B.—Red lesions on sorghum (S. P. I. No. 51976, Rejaf, Sudan) 14 days after spraying with *Bacterium andropogoni* (isolation No. 10, from yellow lesions on another plant of sorghum, S. P. I. No. 51976) at Arlington Experiment Farm, Rosslyn, Va., September 13, 1922. These red lesions were produced by an organism isolated from yellow-brown lesions. × 1.



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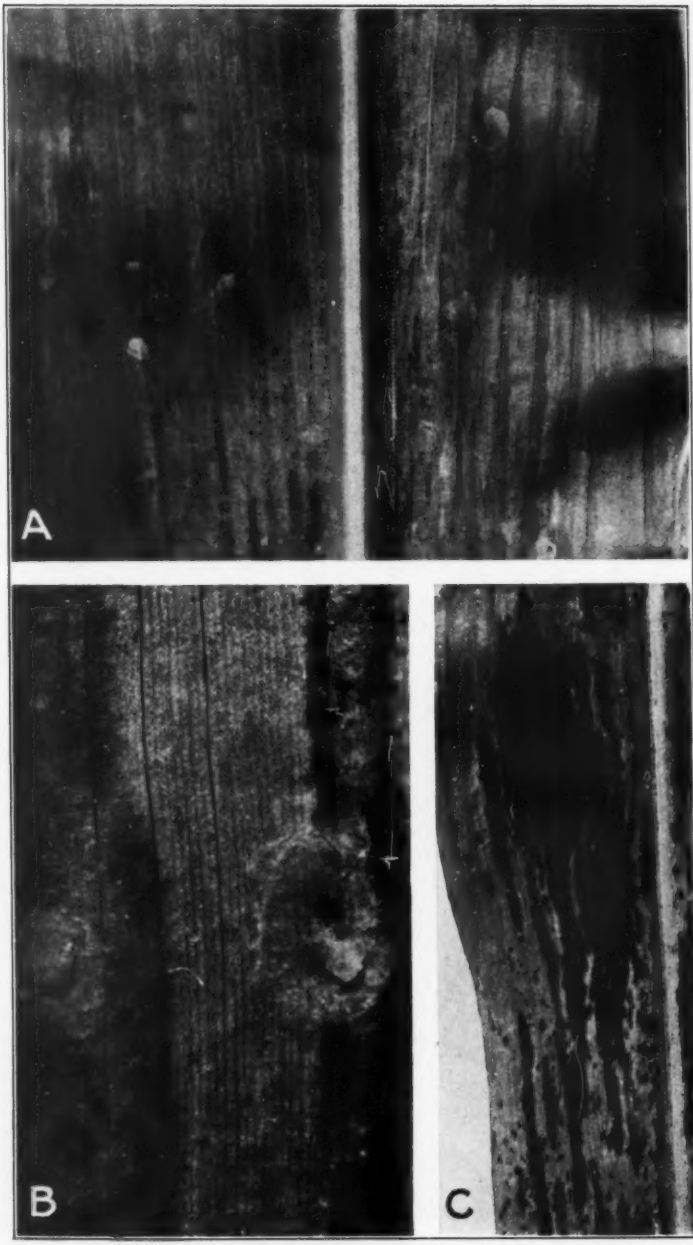


(For explanatory legend see page 7)

compounds. In some of the tests with dextrose the acid production appears to have been masked by the production of alkali.

LITMUS SUGAR AND ALCOHOL AGARS.—Reddening of the litmus occurs with arabinose, galactose, levulose, and dextrose, beginning in 1 to 5 days and reaching the maximum in 8 to 10 days. With glycerin and mannit there also was a trace of reddening after 2 to 3 weeks. There is definite reduction of the litmus with arabinose and dextrose in from 10 to 14 days, and a trace of reduction with galactose after 3 weeks. Saccharose, lactose, and maltose showed no change in reaction and no reduction.

The description here given of *Bacterium andropogoni* agrees with the earlier ones of Smith (*27*, *28*).

VARIETAL RESISTANCE AND HOST RANGE

Hosts for *Bacterium andropogoni* are found naturally in all four classes of sorghum—sorgo, grain sorghum, grass sorghum, and broomcorn (*1*).

During the season of 1922, observations were made on two plots of sorghum at the Arlington Experiment Farm, Rosslyn, Va. One, on upland, contained six varieties of sorgo—Folger's Early, Red Amber, Early Amber, Silvertop, Early Rose, and Sugar Drip. All of these varieties showed infection, varying in degree from light to heavy. Early Rose, Sugar Drip, and Folger's Early had scattered lesions on the lower leaves. The infection on Red Amber was intermediate; that on Silvertop and Early Amber was heavy, many of the lower leaves being badly spotted or destroyed and the lesions extending to the leaves above.

The other plot which was on another section of the farm, contained sorgo and grain and grass sorghums, and was largely a test plot of introduced varieties. Table 2 shows the degrees of infection of the varieties grown in 1922 and 1923.

EXPLANATORY LEGEND FOR PLATE 6

A.—Yellow-brown lesions on sorghum (S. P. I. No. 51978, Rejaf, Sudan) 14 days after spraying with *Bacterium andropogoni* (isolation No. 12 from yellow-brown lesions on sorghum, S. P. I. No. 51978), at Arlington Experiment Farm, Rosslyn, Va., September 13, 1922. Note exudate drops. × 1.

B.—Exudate scales on red lesions on sorghum (S. P. I. No. 51977, Rejaf, Sudan) from natural infections by *Bacterium andropogoni*, at Arlington Experiment Farm, Rosslyn, Va., October 2, 1922. × 10.

C.—Red lesions on feterita × milo (F. C. I. No. 8926) 18 days after spraying with *Bacterium andropogoni* isolated from Sudan grass, September 15, 1923, at Arlington Experiment Farm, Rosslyn, Va. × 1.

TABLE 1.—*Changes in reaction caused by the growth of Bacterium andropogoni in peptone solutions plus carbon compounds*

[Colorometric determinations made]

| Date inoculated and medium used | Inoculated with culture | Incubation period (days) | Hydrogen-ion concentration of medium containing— | | |

| | | |

TABLE 2.—*Susceptibility of different sorghums and related hosts to Bacterium andropogoni at Arlington Experiment Farm, Rosslyn, Va., in 1922 and 1923*

[Degrees of infection: 0=none, 1=trace, 2=light, 3=moderate, 4=heavy]

ON FLATS, 1922 [a]

Variety	Number	Source	Degree of infection
Sorgo:			
Dwarf Early Sumac	F. C.[b] 9500	Selection from S. P. I. 21936, Oklahoma	1
Honey	F. C. 04268	Webster, Kans.	2
Black Amber	F. C. 04269	Jalisco, Mexico	2
Sumac	S. P. I.[c] 35038	Chillicothe, Tex.	3
White	F. C. 9443	Selection from S. P. I. 14724, Bombay, India	3
Silvertop			4
Black Klakah	S. P. I. 54537	Buitenzorg, Java	4
	S. P. I. 54538	do	4
Grain sorghum:			
Gray kafir	S. P. I. 19763	Cedra, Natal	0
Texas Gooseneck	S. P. I. 17553	Chillicothe, Tex.	0
Guinea corn	F. C. 04037	New York, N. Y.	1
Birdproof kafir	S. P. I. 51611	Rhodesia, Africa	4
Chicken corn	F. C. 04020	Henderson, Ky.	4
Durra	F. C. 04251	India	1
Shallu	Agrostology 2650	Plainview, Tex.	1
Unnamed	S. P. I. 55108	Khartum, Anglo-Egyptian Sudan	0
	S. P. I. 55116	do	0
	S. P. I. 55123	do	0
	S. P. I. 55133	do	0
	S. P. I. 55140	do	0
	S. P. I. 55156	do	0
	S. P. I. 55158	do	0
	S. P. I. 55160	do	0
	S. P. I. 55115	do	0
	S. P. I. 55118	do	0
	S. P. I. 55131	do	0
	S. P. I. 55155	do	0
	S. P. I. 55157	do	0
	S. P. I. 55159	do	0
	S. P. I. 55107	do	1
	S. P. I. 55124	do	1
	S. P. I. 55106	do	2
	S. P. I. 55150	do	2
	S. P. I. 51972	Rejaf, Anglo-Egyptian Sudan	2
	S. P. I. 55135	Khartum, Anglo-Egyptian Sudan	3
	S. P. I. 55147	do	3
	S. P. I. 53558	Bombay, India	0
	S. P. I. 51990	Shikaba, Anglo-Egyptian Sudan	1
	S. P. I. 51977	Rejaf, Anglo-Egyptian Sudan	4
	S. P. I. 51980	do	4
	S. P. I. 51976	do	4
	S. P. I. 51978	do	4
	S. P. I. 51983	do	4
	S. P. I. 55127	do	4
	S. P. I. 53561	Bombay, India	1
	S. P. I. 53560	do	3
	S. P. I. 53562	do	4
	S. P. I. 54539	Buitenzorg, Java	2
	S. P. I. 52338	Algiers, Algeria	0
	S. P. I. 53559	Bombay, India	1
	F. C. 04010	Khartum, Anglo-Egyptian Sudan	1
	S. P. I. 51984	Rejaf, Anglo-Egyptian Sudan	2
	S. P. I. 51987	do	2
Grass sorghum	S. P. I. 49697	Bukama, Belgian Congo	1
Unnamed	F. C. 8681	Chuca, Africa	2
	S. P. I. 52025	Rejaf, Anglo-Egyptian Sudan	3
	S. P. I. 52044	Mongalla, Anglo-Egyptian Sudan	0
Sudan grass	S. P. I. 49209	Rhodesia	0

ON UPLAND, 1922

Sorgo:			
Folger's Early			2
Early Rose			2
Sugar Drip			2
Red Amber			3
Early Amber			4
Silvertop			4

[a] Varieties grown by H. N. Vinall, Office of Forage Crops.
[b] F. C. = Forage Crops.
[c] S. P. I. = Seed and Plant Introduction.

TABLE 2.—*Susceptibility of different sorghums and related hosts to Bacterium andropogoni at Arlington Experiment Farm, Rosslyn, Va., in 1922 and 1923*—Continued

[Degrees of infection: 0=none, 1=trace, 2=light, 3=moderate, 4=heavy

ON FLATS, 1923

Variety	Number	Source	Degree of infection
Sorgo:			
Sumac	S. P. I. 35038	Chillicothe, Tex	[d] 2
Red Amber			[e] 3
Orange	F. C. 2208		[d] 2
Black Amber	F. C. 7038		2
White	F. C. 9443	Selection from S. P. I. 14724, Bombay, India	0
Grain sorghum:			
Blackhull kafir	F. C. 03499		0
Chicken corn	S. P. I. 04020	Henderson, Ky	0
Unnamed	S. P. I. 51976	Rejaf, Anglo-Egyptian Sudan	[d] 2
	S. P. I. 51977	do	[d] 2
	S. P. I. 51978	do	2
	S. P. I. 51983	do	0
Yellow milo	S. P. I. 18684	Memphis, Tex	0
Dwarf white milo	F. C. 8927		0
Feterita	F. C. 2314		0
Feterita × milo	F. C. 8926		[f] 0
Manchu kaoliang	C. I. 181 [c]		0
Shallu	Agrostology 2650	Plainview, Tex	0
Broomcorn:			
Standard	C. I. 556		2
Dwarf	C. I. 442		[d] 2
Sudan grass	F. C. 2317		[h] 0
Proso (Early Fortune)	S. Dak. 98		0
German millet	F. C. 2337		0
Corn:			
Field	Unknown		
Sweet (Golden Bantam)	do		

[d] 4 on a few leaves.
[e] 4 on many lower leaves.
[f] 4 artificial on a few leaves.
[c] C. I.=Cereal Investigations.
[h] 2 artificial on a few leaves.

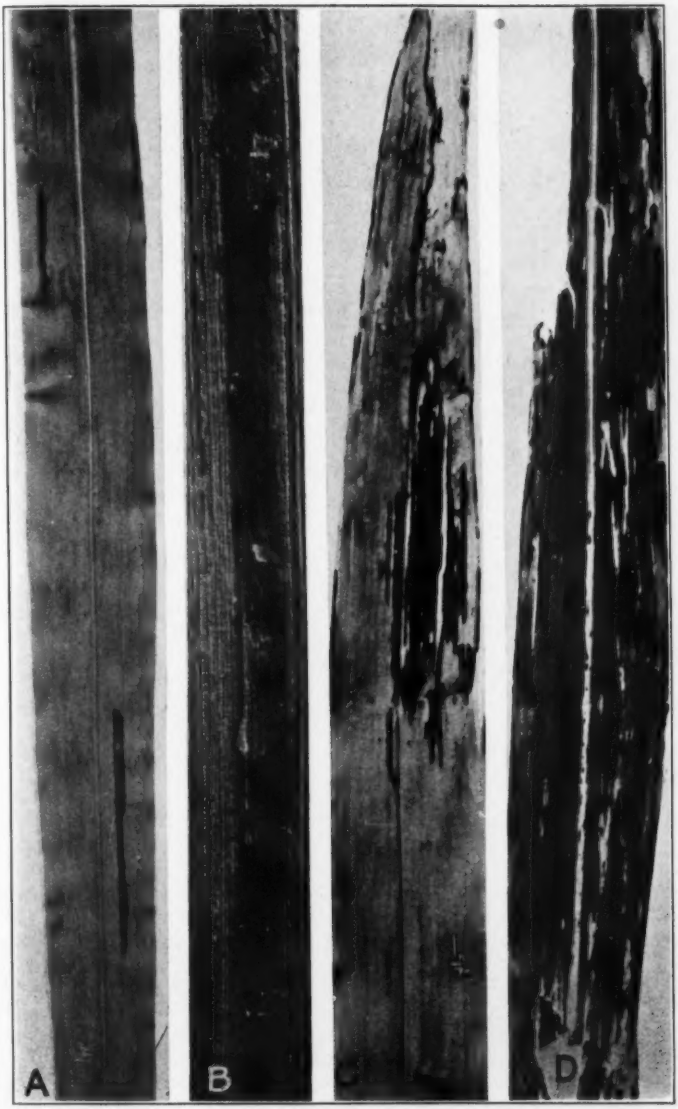
In 1922 the sorgos (sweet sorghums) showed more infection than the grain or the grass sorghums. Of the 8 varieties of sorgo growing on flats all were infected, the infection varying from a trace in 1 variety to heavy in 3 varieties. Silvertop showed heavy infection in both plots. Of the grain sorghums 18 varieties showed no lesions, 9 showed only traces, 6 were lightly infected, 3 moderately infected, and 9 heavily infected. Thus 40 per cent apparently were entirely resistant and 20 per cent heavily infected. Of the grass sorghums, 2, including Sudan grass, showed no infection, and only 1 showed moderate infection. These differences in severity of infection were not due to isolation from, or special contact with, the sources of infection, for entirely resistant varieties grew between and with leaves touching those of moderately to heavily infected varieties. The grass sorghums showed no very susceptible variety and appeared to be more resistant than the other two groups.

The season of 1923 was much less favorable than that of 1922 for bacterial infection because of the drier weather. The experimental plot at the Arlington farm included not only sorgos, grain sorghums, and grass sorghums, but also broomcorn, millet, field corn, and sweet corn, grown in the hope of testing further the host range of the disease and varietal susceptibility and resistance. While there were some interesting developments, the results of this season's work in the field are not to be considered conclusive, because of the unfavorable weather. Varieties that showed heavy infection in

1922 showed very little in 1923, even after repeated attempts had been made to produce artificial infection by spraying with pure cultures. All of the sorgos except one showed some infection. There was little infection on the grain sorghums. The kafirs, milos, feterita, kaoliang, and shallu showed no infection, although sprayed several times with water suspensions of pure cultures. But as some of these, chicken corn and shallu for instance, had shown considerable infection the year before, all would have to be tested under more favorable weather conditions before a definite conclusion as to their resistance could be reached. Several leaves of a feterita-milo hybrid sprayed with a pure culture became heavily streaked with the disease. Natural but light infection appeared on Dwarf broomcorn, and toward the end of the season some of the lower leaves were heavily streaked with dark-red lesions. Standard broomcorn formed a part of the same row with a dwarf variety but appeared to be more resistant. When this row was sprayed with pure cultures a light infection was produced. Lesions on Dwarf broomcorn were dark red, but on the Standard variety they were lighter and more orange-red.

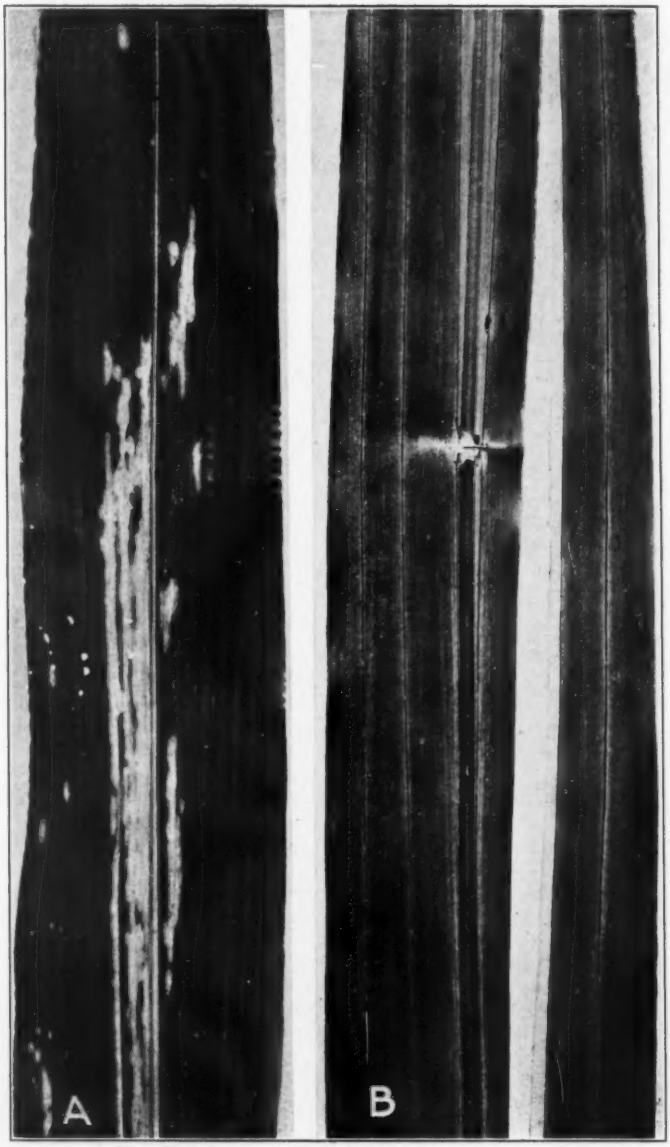
While natural infections with *Bacterium andropogoni* occur on some of the grass sorghums, none were observed at first on Sudan grass. In the latter part of August, 1923, Sudan grass and other varieties in the plot at the Arlington farm were sprayed with a water suspension of culture No. 10. About three weeks later a few lesions were found which looked like the bacterial lesions on sorghum. (Pl. 7, A.) They were deep purplish red throughout, 2 to 4 or more centimeters long by a few millimeters wide, and covered with exudate scales. (Pl. 7, B.) Bacteria streamed from sections under the microscope, and isolations produced typical colonies of *Bact. andropogoni*, which on reinoculation again produced the same type of lesion on Sudan grass and on a feterita–milo hybrid. (Pl. 6, C.) This type of lesion on Sudan grass is of interest because it is entirely different from the type so common on Sudan grass, viz, oval spots with tan or light-brown centers and narrow red margins. During the season of 1924 natural infections caused by *Bact. andropogoni* were found on Sudan grass growing at the Arlington farm and at Manhattan, Kans. (Pl. 7, C, D.) The lesions were the typical dark-red streaks with scales of dried exudate, and in the plot at Manhattan the infection was general and abundant on at least 50 per cent of the plants. On proso (Early Fortune, S. Dak. No. 98) and on German millet no lesions were produced even after repeated sprayings. Several inoculations were made on Eureka field corn and Golden Bantam sweet corn at the Arlington farm and at Tuxedo, Md., during 1923, but with negative results.

In the greenhouse an unidentified field corn known as "First of All" and Golden Bantam and Stowell Evergreen sweet corns were sprayed and negative results obtained. Finally another variety of field corn, Boone County White (C. I. 119), was sprayed in the greenhouse in January, 1924, and placed in a damp chamber. Two different inoculations on several plants gave positive results (pl. 8, A), while checks sprayed with sterile water and treated in the same manner remained unspotted. Lesions began to appear after three to four days as water-soaked streaks 1 to 2 cm. long and 1 to 2 mm. wide. These lesions in some instances became 8 cm. long and turned brown as they grew older. There were evidences of exudate, and bacteria streamed from sections under the microscope. Isolations from these



A and B.—Red lesions on Sudan grass (F. C. I. No. 2317) 26 days after spraying with *Bacterium andropogoni* (isolation No. 10, from yellow lesion on sorghum, S. P. I. No. 51976), at Arlington Experiment Farm, Rosslyn, Va., August 20, 1923. A, × 1; B, one lesion, × 10, showing scales of exudate.

C and D.—Natural infection on Sudan grass with *Bacterium andropogoni* at Arlington Experiment Farm, Rosslyn, Va., September 18, 1924.



A.—Infections on Boone County White corn (C. I. 119) 16 days after spraying with *Bacterium andropogoni* (isolation No. 32 from sorghum, S. P. I. No. 51976) in greenhouse at Washington, D. C., collected and photographed April 2, 1924.

B.—Infections, narrow red streaks with yellowish green margins, 40 days after spraying Hawaiian Striped Tip cane with *Bacterium andropogoni* (isolation No. 76 from Dwarf Java sorgo, S. P. I. No. 39269) in greenhouse at Washington, D. C., December 16, 1924.

lesions produced pure cultures of the typical sorghum organism, which in two inoculations on sorghum resulted in typical red lesions. *Bacterium andropogoni* was reisolated from these sorghum lesions. It appears that some varieties of corn are susceptible to infection with this organism.

Water suspensions of sorghum isolations Nos. 8 and 9 which were sprayed into uninjured sheaths of Lahaina sugar cane growing in the greenhouse caused no infection. Two years later suspensions of cultures of sorghum isolation No. 33 were sprayed on leaves of sugar cane that had been pricked with a needle. Narrow red stripes 2 to 3 inches long developed on all three varieties—D 117, Louisiana Purple, and Uba. Isolations from these red lesions produced pure cultures of the sorghum organism. Water suspensions of three sorghum isolations were pricked into Hawaiian Striped Tip cane. Checks showed no reddening or streaks, but on inoculated leaves narrow red stripes 6, 8, or 10 inches long developed from the punctures along the veins. (Pl. 8, B.) The tissue on either side of the red stripes tended to lose its green color. Pure cultures of the sorghum organism were isolated from one of these lesions. Evidently there is a wide host range for *Bact. andropogoni* among the sorghums, but a more favorable season or seasons are necessary for determining just what groups or varieties are resistant and whether the host range extends naturally outside of the sorghums. While artificial infection may be induced with *Bact. andropogoni* on some varieties of corn and sugar cane, the lesions develop slowly and so far as observed never increase much in size.

COMPARISON WITH SIMILAR DISEASES

EARLY LITERATURE [4]

In 1883 Palmeri and Comes (*19*) in Naples published a brief paper describing a disease of sorghum that was characterized by an intense red stain and a spontaneous alcoholic fermentation of the juice of the cane. The red color occurred in the tissues of the internode and in the sheath of the corresponding leaf or only in the leaf sheaths. Microscopic examination revealed two colorless microorganisms—one elliptical, 5–7 by 2–3 μ, which reproduced by budding, and the other spherical, scarcely 1 μ long, and actively motile. The larger one, they say, corresponds perfectly to the species named *Hormiscium sacchari* by Bonorden and later named *Saccharomyces ellipsoideus* by Rees. The smaller organism they refer to *Bacterium termo* Djrd. They thought that the yeast started the alcoholic fermentation and then the bacteria destroyed the tissue, but their statements are based on speculation and not on experimental proofs. In 1884 Cowgill (*11*) made an analysis of juices of canes injured, he says, by parasitic fungi in Kansas. Kellerman and Swingle (*15*) considered this the same disease described by them as due to *Bacillus sorghi*. Specimens sent them at the time showed the characteristic stains of the disease.

In 1887 Burrill (*4*) described a disease of broomcorn and sorghum, in Illinois, that has been supposed by some to be the same as that observed by Palmeri and Comes in Italy. He described the most

[4] Condensed from a discussion of literature written by Erwin F. Smith about 1908.

conspicuous symptoms as red blotches on leaves and leaf sheaths, which later spread to the stalks and the brush of broomcorn. The roots became red and decayed and the stalks were easily lifted from the soil. He found bacteria uniformly associated with the disease, and he and his students isolated from both roots and aerial parts a form that was believed to be the cause of the disease. On plate cultures the characteristic growth was white or pearllike with lobed and fimbriate margins. The organism did not liquefy gelatin but was described as growing well in beef broth, in infusions of potato and of maize kernels, and upon nutrient gelatin and agar. Spore formation was described in detail. The size of the rods varied from 0.5–1.0 by 1.0–3.0 μ. Successful inoculations were made upon young plants, both from macerations of old material and from pure cultures of the bacillus. Liquid cultures smeared upon the leaves produced red flecks at the stomata in 48 hours and later made the leaves red mottled. The red coloring was attributed by Burrill to chemical decomposition of the cell contents. He states that the organism was reisolated in pure culture and again produced the disease. In another publication (*5*) he named the organism *Bacillus sorghi* n. sp. M. B. Waite, who did part of this work, told Smith in 1900 that he was skeptical about the results of the inoculations for the reasons that the tiny spots obtained from the inoculations did not enlarge readily into the typical spots of the disease as it appeared in the field and that any injury on sorghum or broomcorn is likely to be followed by a red stain.

In 1888 Kellerman (*14*) published a preliminary report on sorghum blight, and in 1889 Kellerman and Swingle (*15*) published a paper identifying the Kansas disease of 1888 with that reported from Illinois. From their colored figures it is not clear whether they actually had Burrill's disease under observation, but it is probable that they did. The red blotches and spots on the leaf sheaths shown in Plates I and II (*15*) are unlike the bacterial disease of sorghum studied in Washington and suggest strongly the action of chinch bugs and aphids. The inside of the sheath is the favorite feeding ground of these insects, the result of their presence being red blotches and spots. Plate III (*15*) shows seedling plants spotted as the result of artificial infections, but the slight infections shown are not at all convincing.

The injuries due to the disease are described as irregular elongated red or reddish blotches on leaves, leaf sheaths, and roots. The red discolorations were more numerous and brighter on the inner surfaces of the sheaths, where the discolorations invariably first appear. The blotches are sometimes limited laterally by the large longitudinal veins and at other times widen out and involve the whole surface. A very faint orange discoloration is the first indication of the disease. This color deepens to shades of red until the lesions finally become very dark or almost black.

Frequently, but not invariably, there were leaf lesions, elongated bands of discoloration irregularly limited by the veins of the leaf. In some cases the patches were regular in shape and distribution and all the leaves of the plant were similarly and abundantly marked. They seemed to think it probable that all the symptoms they described were not referable to the same disease. When the disease was severe, complete destruction of the sorghum plants resulted, but when mild, the growth was only slightly checked. Seventy-

five to ninety per cent of the plants in some varieties were destroyed, while other varieties remained uninjured.

They considered *Bacillus sorghi* as the cause of the disease—a spore-bearing organism unlike *Bacterium andropogoni* but resembling that described by Burrill (*5*). The cells are 1.33–4.0 μ by 0.5–1.25 μ Spore formation is described in detail much as by Burrill. On agar and potato the typical color when young is pearly white, though there is sometimes a slight tinge of yellow or pink. When very old the colonies are a dirty white and very much wrinkled. Potato and agar cultures were inoculated directly from diseased sorghum plants. Apparently none of the cultures were started from poured-plate colonies or from dilutions. They state that of the nine sorghum plants inoculated six showed slight red stains. There is no record of any studies being made to determine whether the tissues thus reddened on the inoculated plants were occupied by bacteria, and no cultures were made from these spots for further inoculations.

It is probable that Kellerman and Swingle's field observations (*15*) relate to Burrill's disease. They agree in ascribing the disease to a spore-bearing organism, which may be the same as Burrill's *Bacillus sorghi*. However, they may have had a mixture of parasites, this being one and that described by the writers another, or they may have dealt only with insect injuries complicated by various saprophytic bacteria.

The few inoculations do not afford conclusive evidence as to etiology, since some plants did not take the disease, and others were already beginning to show local injuries and red stains when inoculated. It is quite possible, therefore, that the latter would have developed the other injuries described and figured if nothing had been done to them, i. e., as the result of punctures of aphids or other insects. In general also the spots appeared too soon (the third day on the young plants) to be due to the organism described as *Bacterium andropogoni*, and they did not continue to enlarge.

Swingle stated in personal conference in 1900 that he was likewise skeptical as to the value of the infection experiments on sorghum as given in the paper by Kellerman and himself (*15*), all the necessary precautions not having been complied with.

In 1883 Palmeri and Comes (*19*) mentioned briefly, as we have seen, that a yeast was found in the reddened pith, and also a bacterial organism, which was likened to *Bacterium termo* Djrd. At that time these authors were evidently inclined to think the disease due to the yeast, because there was alcoholic fermentation in the stems, and because the bacterium was mentioned as something occurring "later" than the alcoholic ferment, which is said to be "first." Neither organism was described properly, or cultivated, and no inoculations were made. In 1884 Comes (*9*) stated in a footnote that the sorghum disease was due to *Clostridium butyricum*. On the appearance of the papers by Burrill and by Kellerman and Swingle, Comes (*10*) came forward with claims of priority for his discoveries. These were answered by Kellerman and Swingle (*16*) and by Burrill (*6*).

How Comes could identify the schizomycete *Clostridium butyricum* with a budding yeast measuring 2–3 by 5–7 μ, and originally stated by him to be exactly like *Hormiscium sacchari* Bonorden, and probably identical with *Saccharomyces ellipsoideus* Rees, is more than

one is able to explain. Moreover, *C. butyricum*, so far as known, is a strict anaerobe and does not destroy cane sugar with the production of ethyl alcohol; morphologically it is also quite unlike the schizomycetous form mentioned by Comes and likened to *Bacterium termo* Djrd.

According to Brizi (*2*), this disease also occurs on maize in Italy. The disease he described was prevalent in Romagna in 1893 and was characterized by the presence of large or small spots, which were reddish to bright red at first, becoming wine red with age. In the earliest stage, on young plants, the spots were pellucid, then yellowish, then bright red, then dark red, the entire plant finally drying out. These blotches appeared on all parts of the plant but were most frequent and most injurious on the leaf sheaths, lower leaf blades, and the rachis of the ears, rather than on the roots. If the plants were attacked while young the ears remained small, contorted, and atrophied. On better developed ears a part of the kernels dried out and blackened, even when there was no external indication of disease. No mention is made of any insect injuries. *Cladosporium herbarum* was observed only on leaves already dead. The field examinations appear to have been limited to one week in August. The disease is said to have all the characteristics of the American sorghum blight of Burrill and Kellerman. A microscopic examination of the diseased parts (base of stem and leaf sheaths) showed the protoplasm contracted and the cavities of the cells filled with bacteria, which were, it is said, in all respects like *Bacillus sorghi*. The walls of the cells did not show any structural change but were stained light red. As no cultures or inoculations were made, the relation of this Italian disease to other diseases is uncertain.

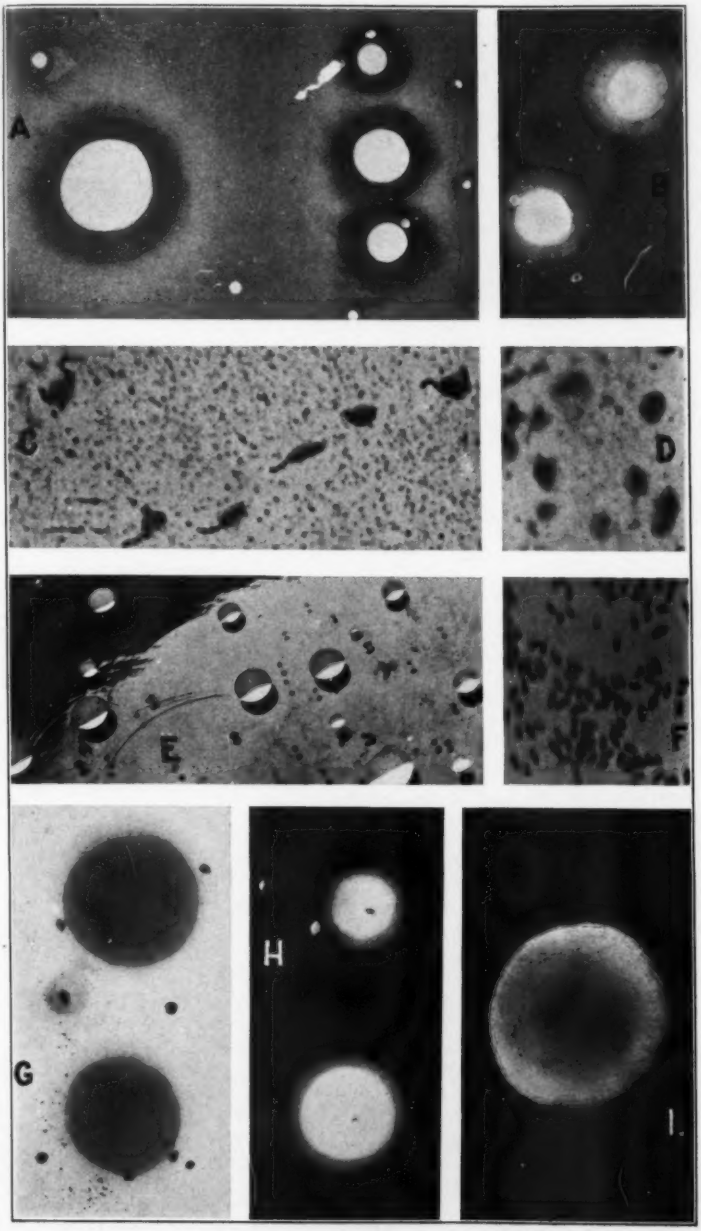
In 1893 Cavara (*8*) published a paper on a disease of sorghum found in Ancona, Italy, that was characterized by orange or red spots on the sheaths. He identified this disease as the one described by Comes and described from it a new species of yeast, *Saccharomyces comesii*.

In 1893 Passerini (*20*) published a note on the nature of the coloring matter occurring in the reddened leaf sheaths of sorghum and named it sorghina. In a subsequent paper (*21*) he stated that the pigment as it occurs in the plant is not the same as his sorghina, and proposed for the unchanged pigment the name sorgorubina. It is stated in a footnote that while he always found bacteria in the large old spots he was not able to find them in the small young ones, and also that he had induced the spots by inoculating with the bacteria. These statements, however, are of no great value, inasmuch as he disclaims any special knowledge of bacteriology and says that further studies should be made.

EXPLANATORY LEGEND FOR PLATE 9

Cultures of *Bacterium andropogoni*

A.—Colonies on beef-peptone agar, showing halos in agar. Photographed September 27, 1922. × 1½.
B.—Two 5-day gelatin colonies, March 26, 1923. Dense centers and thin margins. Grown at 18° C. ×5.
C.—Smear from a 2-day agar culture. Casares-Gil flagella stain, March 27, 1924. × 1,900.
D.—Smear from a 2-day agar slant. Capsules. Casares-Gil stain, January 17, 1924. × 1,500.
E.—Several 5-day agar colonies from sorghum (S. P. I. No. 51978), August 29, 1922. × 1½.
F.—Smear from 2-day agar streak of sorghum No. 33. Stained with gentian violet, January 16, 1924. × 1,900.
G.—A few 20-day agar colonies photographed by transmitted light, showing thin margins, August 29, 1922. × 10.
H.—Some 9-day colonies photographed by transmitted light, showing clear margins, October 4, 1922. × 3.
I.—A 5-day colony on beef-peptone agar photographed by transmitted light, showing irregularly concentric internal markings, March 12, 1923. × 10.



(For explanatory legend see page 16)

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In 1898 Bruyning (*3*) published a paper on sorghum blight and the bacteria which cause it. It is impossible to decide from his lithographic figures whether or not he had under consideration the disease described by Burrill. The probability is that he did, but having a strong prepossession that the organism causing the disease must be a red or yellow schizomycete, he seems to have paid little attention to any others. He made no inoculation experiments and no careful study of insect injuries. He saw the disease in the summers of 1896 and 1897 at Wageningen, Netherlands, where sorghum plants were grown from seed obtained in Naples. The symptoms of the disease consisted of spots and blotches on the leaf sheaths and the stems, these being more or less deep red brown. The attacked leaves had a tendency to split longitudinally as if torn by the wind. On the stem above the nodes there were often observed spots of clear brown, reddish brown, or deep scarlet red, irregular in form. None of Bruyning's colored illustrations show any scarlet spots, but possibly the lithographer may have been at fault. Bruyning says that most often the disease appears first on the inner face of the leaf sheath as yellowish elongated spots, which enlarge, fuse, and redden until the entire inner surface is blotched and dark red. The stem under the sheath also becomes diseased, the pith is stained, the roots are always attacked, and the glumes are frequently spotted. The symptoms described indicate complications due to insect injuries.

On microscopic examination Bruyning found bacteria in enormous quantities in the diseased tissues. He seems to have examined them mostly in juice squeezed from the affected tissues, although he obtained the same results from an examination of fresh sections. He described two new species of microorganisms from these spots. His *Bacillus ruber ovatus* is a short, nonsporiferous rod, occasionally in short chains, sometimes feebly motile, producing on potato in four days beautiful vermilion spots with all transitions to coral red. It grew very slowly in bouillon, was strongly aerobic, and did not liquefy gelatin. It bleached slowly, sometimes very slowly, by Gram's method.

The other species of Bruyning is *Micrococcus aurantiacus sorghi*. This is a coccus or a cocciform bacillus, smaller than the preceding species. It occurs many times as a diplococcus, and in chains of 10 or 12, especially in bouillon, and is doubtfully motile. On potato it forms yellow spots which become golden and gradually brownish. It grows rapidly, so that at the end of three weeks the colonies have diameters of 3 to 4 cm. It is slightly viscous and destroys starch. The color of the potato remains either unchanged or becomes a grayish lead or brownish color. In less than three days in milk there is a separation of the whey. At the end of about seven days the casein begins to coagulate. This organism grows more rapidly in bouillon than the preceding species and forms a light-gray deposit. In litmus gelatin there is an abundant formation of acid, which was not true in tests with the other species. Gelatin is not liquefied, or only very feebly so after three or four weeks.

It seems never to have occurred to Bruyning to bruise or otherwise wound the sorghum plants to see whether that of itself would cause them to take on a red coloration. He (*3*) reasons that in a disease characterized by the production of intense pigment the bacteria that produce it should also show the power of pigment production upon some of the substrata used for the growth of pure cultures.

Therefore Burrill's bacillus could not be considered the specific agent of sorghum blight. *Bacillus ruber ovatus* and *Micrococcus aurantiacus sorghi* did produce pigment on nutrient media. The micrococcus, since it produced golden-yellow spots on potato and was a rapid grower, Bruyning associated with the early stages of the disease. The slower growing bacillus, which produced vermilion spots on potato, he associated with the later stages. But since he made no inoculation experiments, he did not demonstrate that these two organisms have any connection with the disease.

In 1899 Radais (*22, 23, 24*) described a disease of sorghum which he identified as that of Palmeri and Comes. The diseased plants, which were stained an intense red, came from Algeria. Radais found in these plants only a yeast and determined it to be pathogenic by pure-culture inoculations, but as the host plant is much inclined to redden when injured, it is not denied by him that other parasites such as bacteria may cause similar phenomena. Pure cultures of this yeast on various media were creamy white, and exception is taken very properly to Bruyning's statement that organisms that are not chromogenous on culture media can not be the cause of this disease.

In 1904 Busse (7) published an investigation of a disease or diseases of sorghum characterized by the same symptoms as those mentioned by Burrill, Kellerman and Swingle, and Bruyning. He saw the disease first in the German territory of East Africa, where it was very serious in 1899 and subsequent years. He does not, however, appear to have made any extensive study of it there, but at Buitenzorg, Java, with plants grown from sorghum seed obtained in Africa, he carried on studies in the fall and winter of 1900–1901 making many careful microscopic examinations. It does not appear from his long paper that he made any pure cultures or attempted to make inoculations.

Busse discovered in sorghum plants attacked by *Aphis adusta* a bacterial rot of the tender apex, but only in cases where the aphid had been previously present abundantly. This insect affects, mostly, the still undeveloped, rolled-up, inner leaves of the sorghum. The other aphid abundant in Java on sorghum is the common plant louse of sugar cane, *A. sacchari*, which is likely to be found on all green parts of the plant, and here the injury was followed by the customary red and brown spots, blotches, and stripes.

In a few cases in Java, Busse observed reddening of the midrib, and a multiplication of bacteria in the intercellular spaces, which he says could not be connected with any aphid punctures of either the midrib or the adjacent blade of the leaf, nor with stomatal infection. The bacteria multiplied first, he thinks, on minute quantities of substance diffused out of the cells, and subsequently by enzymic action or otherwise on the middle lamella or on the cellulose wall. How they entered the leaf was not determined.

Busse states that the corrosion of the leaf sheath, exclusive of those cases where the bacteria enter by the puncture of the aphids, always begins in the stomata. Like Burrill, Kellerman and Swingle, and Bruyning, he describes the disease as beginning on the inside of the leaf sheath. The inside of the sheath may be very strongly attacked by the disease, while the corresponding places on the outside are very little stained. Like Bruyning, he found coccuslike forms abundant in the diseased tissue.

Busse considered the red color to be a plant reaction to wounds and injuries of various kinds. He obtained it by painting the surfaces of the leaves with turpentine and various other chemical substances. His colored lithographic figures showing characteristic spots and blotches on stems and leaves are a more brilliant red, but otherwise are much like those of Kellerman and Swingle.

The general conclusion of Busse is that there is no bacterial disease of sorghum in any true sense of the word, but only a disturbance caused by aphids complicated by the presence of saprophytic bacteria multiplying enormously in the excretions of the insects and infesting the vicinity of the wounded tissues semiparasitically owing to the nourishment offered them.

This was the early opinion of Smith regarding the red spotting of sorghum. Published papers were not convincing, and frequent opportunities to examine red-blotched broomcorn and sorghum always showed the leaf-sheath injuries to have been preceded by the attacks of aphids, which insinuated themselves through very small openings, formed colonies under the leaf sheath, and created conditions very favorable for the multiplication of bacteria. If the aphids were not there at the time of examination, they had generally left indications of their previous presence in the form of cast-off skins and remnants of their bodies. The bacteria that were present appeared to be saprophytes or at least very feeble parasites. It was therefore a matter of no small interest that in 1904 in the District of Columbia a serious disease of sorghum and broomcorn was found that could not be considered as simply a saprophytic invasion of badly wounded tissues, but that behaved like other typical bacterial diseases; that is, it could be reproduced at will typically in all its phases with pure-culture inoculations in the absence of insects.

Clearly this was not wholly Comes's disease, Burrill's disease, Kellerman and Swingle's disease, or Bruyning's disease. It is possible, even, perhaps probable, that it was partly their diseases; that is, that they confused this disease with other diseases manifesting themselves in the form of red blotches. Incomplete descriptions and lack of numerous clean-cut, convincing infection experiments make it difficult to decide. Clearly Burrill's descriptions of *Bacillus sorghi* do not agree with the characteristics of the parasite described in this paper, and since it was possible that, with further study of the combined action of insect and bacteria, *B. sorghi* might be again found and demonstrated to be the principal bacterial agent in this form of disease, it seemed best to recognize three red diseases of sorghum: (1) The yeast disease of Comes, first carefully described by Cavara (*8*) and especially by Radais (*22, 23, 24*); (2) the blotch disease of leaf sheaths, etc., due primarily to injuries by aphids and other insects, complicated by bacteria of various sorts, rods (Burrill, (*5*) Kellerman and Swingle (*15*)), cocci and rods (Bruyning (*3*), Busse (*7*)); and (3) the disease worked upon in the United States Department of Agriculture and described as due to *Bacterium andropogoni*.

RECENT LITERATURE

In addition to these early accounts of sorghum diseases, four more recent descriptions of bacterial diseases are of interest.

Serbinoff (*26*) in 1915 named *Bacillus omelianskii* as the cause of a soft rot of the stems of sorghum plants sent from Tashkend and Samarkand in the steppe regions of western Asia. Specimens from three different localities showed a darkening and rotting of the lower part of the stem just above the roots. A characteristic and disagreeable odor of butyric acid was given off from the rotting stalks. A dark-brown slimy liquid flowed from the diseased tissue and filled all the intercellular spaces. Bacteria were found constantly associated with the disease. From stained smears made directly from diseased tissue the organism was found to be a nonmotile, spore-forming, Gram-positive rod. The organism was not grown in pure culture and there is no record of inoculations. Neither the symptoms of the disease nor the brief description of the organism agrees with the descriptions of the disease caused by *Bacterium andropogoni*.

Recent papers by Kendrick (*17*, *18*) name and describe *Bacterium holci* as the cause of spotting of *Holcus* sp., *Zea mays*, *Pennisetum glaucum*, and *Chaetochloa lutescens*. The lesions are not always the same in form, varying from round or oval to linear or irregular, and are either red or light centered with red borders. The organism liquifies gelatin, reduces nitrates, and differs in other important characters from *Bact. andropogoni*.

A bacterial red-stripe disease of Hawaiian Striped Tip canes was described by Lee and Jennings (*13*) in 1925. On the cane leaves the lesions were long, narrow, and dark red, with longitudinal streaks that look much like the lesions produced on sorghum by *Bacterium andropogoni*. The causal organism, *Phytomonas rubrilineans*, however, differs from *Bact. andropogoni* in important characters. It is a facultative anaerobe, is pale yellow on agar, liquefies gelatine and reduces nitrates. These authors report that on cane inoculations with *Bact. andropogoni* gave negative results and that on sorghum inoculations with the cane organism produced lesions that were not characteristic of the sorghum blight. While the authors were able to produce with *Bact. andropogoni* the slight infections on Hawaiian Striped Tip cane shown in Plate 8, B, no characteristic lesions such as Lee described and figured were ever obtained.

ECONOMIC IMPORTANCE AND DISTRIBUTION

The lesions caused by *Bacterium andropogoni* occur mostly on the leaves. Any injury to the plants would be occasioned by the destruction of the tissue that elaborates the plant food. During warm moist seasons, which are particularly favorable to the development of the disease, lesions may spread from the lower to the upper leaves until one-half to two-thirds of the leaf surface is destroyed in susceptible varieties.

As the bacteria are carried by water and by air currents from one leaf to another, and probably also by insects, they could very easily be carried in this way from the upper leaves to the heads. It is quite probable that the disease is carried over on the seed from season to season, as it develops in fields that have not been previously sown to sorghum. The spread of the disease from one plant or row to surrounding plants and rows often has been observed in the field. Several attempts to isolate the organism from red spots on the seed have given negative results.

SUMMARY

A bacterial disease of broomcorn and other sorghums (*Holcus sorghum* L.), producing red streaks and blotches on the leaves and showing abundant exudate in the form of dried scales, was described by Smith and Hedges in 1905. In 1911 Smith, after a brief characterization of the causal organism, named it *Bacterium andropogoni*.

The lesions occur mostly on the leaves and may be destructive. The distinguishing characters of the disease caused by this organism are elongating red stripes, in which the red color is not marginal but continuous throughout the lesion, and an abundant exudate in the form of red flakes or scales on the under surfaces of the leaves. The infections are stomatal, but also may be produced by wounds.

Inoculation experiments and observations in the field have shown that some varieties are susceptible and others resistant to the disease. Infections have been artificially produced on maize and sugar cane. *Bacterium andropogoni* is a polar flagellate, nonliquefying, nonsporiferous, nonnitrate-reducing, slow-growing, viscid, white organism, distinct culturally and morphologically from the other bacterial organisms recorded as causing blighting of sorghum. With pure cultures of this organism the typical disease was reproduced in the hothouse in 1904–5 and again in the hothouse and more abundantly in the field in 1922–23.

LITERATURE CITED

(1) Ball, C. R., and Rothgeb, B. E.
1918. grain-sorghum experiments in the panhandle of texas. U. S. Dept. Agr. Bul. 698, 91 p., illus.

(2) Brizi, U.
1894. prime indagini intorno ad una nuova malattia del granturco osservata in romagna. Bol. Not. Agr. (1893) 15: 563–564.

(3) Bruyning, F. F., Jr.
1898. la brûlure du sorgho (maladie du sorgho sucré, sorghum blight, hirsebrand, sorghum-roodziekte), et les bactéries qui la provoquent. Arch. Néerland. Sci. Exact. et Nat. (2) 1: [297]–330, illus.

(4) Burrill, T. J.
1887. a disease of broom-corn and sorghum. Soc. Prom. Agr. Sci. Proc. 8: 30–36.

(5) ———
1887. "disease germs." another illustration of the fact that bacteria cause disease. Microscope 7: [321]–331, illus.

(6) ———
1889. [status of the sorghum blight.] Jour. Mycol. 5: 199. (Reply to criticisms by O. Comes.)

(7) Busse, W.
1904. untersuchungen über die krankheiten der sorghum-hirse. ein beitrag zur pathologie und biologie tropischer kulturgewächse. Arb. K. Gsndhtsamt., Biol. Abt. 4: [319]–426, illus.

(8) Cavara, F.
1893. sopra un microorganismo zimogeno della durra (sorghum caffrorum p. b.). Agr. Ital. 19 (261): 7. [Abstract in Rev. Mycol. 15: 137–139. 1893.]

(9) Comes, O.
1884. il marciume delle radici e la gommosi della vite. 32 p. Napoli.

(10) ———
1889. una rivendicazione di priorità sulla malattia del sorgo saccarino. (Abstract.) Rend. R. Inst. Incoragg. Napoli 7/8:1–5.

(11) Cowgill, E. B.
1885. The sorghum industry of Kansas in 1884. Kans. State Bd. Agr. Bien. Rpt. (1883/84) 4: 622–633.
(12) Elliott, C., and Smith, E. F.
1924. A bacterial disease of broomcorn and sorghum. (Abstract.) Phytopathology 14: 48.
(13) Hawaiian Sugar Planters' Association Experiment Station, Department of Pathology.
1925. Red-stripe disease studies. 99 p., illus. Honolulu, Hawaii.
(14) Kellerman, W. A.
1888. Preliminary report on sorghum blight. Kans. Agr. Expt. Sta. Bul. 5: [56]–60.
(15) ——— and Swingle, W. T.
1889. Sorghum blight. Kans. Agr. Expt. Sta. Ann. Rpt. (1888) 1: 281–302.
(16) ——— and Swingle, W. T.
1889. Status of the sorghum blight. Jour. Mycol. 5: 195–199. (Reply to criticisms by O. Comes.)
(17) Kendrick, J. B.
1926. Holcus bacterial spot on species of holcus and zea mays. Phytopathology 16: 236–237.
(18) ———
1926. Holcus bacterial spot of zea mays and holcus species. Iowa Agr. Expt. Sta. Research Bul. 100, p. 303–334, illus.
(19) Palmeri, P., and Comes, O.
1883. Notizie preliminari sopra alcuni fenomeni di fermentazione del sorgo saccarino vivente. Rend. R. Accad. Sci. Fis. e Mat. Napoli 22: 310–312.
(20) Passerini, N.
1893. Sopra una materia colorante rossa atta alla tintura dei tessuti che può estrarsi dalle foglie della commune saggina. Atti R. Accad. Econ. Agr. Georg. Firenze (4) 16: [52]–61.
(21) ———
1897. Sopra la sorghina e la sorgorubina.—Breve nota. Bul. Soc. Bot. Ital. 1897: 195–197.
(22) Radais, [M.]
1899. Le parasitisme des levures, dans ses rapports avec la brûlure du sorgho. Compt. Rend. Acad. Sci. [Paris] 128: 445–448.
(23) ———
1899. La brûlure du sorgho sucré. Bul. Soc. Mycol. France 15: [82]–89.
(24) ———
1899. On the blight of sorghum. Bot. Gaz. 28: 65–68.
(25) Ridgway, R.
1912. Color standards and color nomenclature. 43 p., illus. Washington. D. C.
(26) Serbinoff, J. L.
1915. Bacillus omelianskii nov. sp. nouveau microbe butyrique, comme instigateur "gummose bacillaire" du sorgho. Zhur. Bolĕzni Rast. 9: [95]–113, illus. [In Russian. French résumé, p. 112–113.]
(27) Smith, E. F.
1905–11. Bacteria in relation to plant diseases. v. 1–2, illus. Washington, D. C. (Carnegie Inst. Wash. Pub. 27.)
(28) ——— and Hedges, F.
1905. Burrill's bacterial disease of broom corn. (Abstract) Science (n. s.) 21: 502–503.
(29) Society of American Bacteriologists, Committee on Bacteriological Technic.
[1923]. Manual of methods for pure culture study of bacteria. A48 p., illus. Geneva, N. Y.

THE CAPILLARY STRUCTURE OF SOFTWOODS[1]

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INTRODUCTION

The investigations reported in this paper form a possible basis for further studies in fields other than the one in which the work was done. Methods similar to those employed in these investigations, for instance, may assist the plant physiologist in his study of the movement of liquids and gases through plant tissues. By means of these methods some fundamental measurements of wood structure were made on a scale much larger than that practical with a microscope, and other measurements that are beyond the limit of our present microscopes were made with a reasonable degree of certainty. Further, the results already secured by means of the application of these methods to wood structure are of interest also in a consideration of other plant structure.

The woods employed in the experimental work were selected as typical softwoods except that they are comparatively free from resin ducts; other similar species perhaps would have been as representative of the group. Because in this work each should be considered as a typical softwood rather than as a particular species, the names in general use have been chosen for the report in preference to the exact botanical names of the individual species. The names that appear are the standard common names adopted by the Forest Service of the United States Department of Agriculture (*36*)[2].

The symbols used have the following meanings:

Δ = a small increment of.
ζ = contact potential of wood in contact with water.
η = viscosity of a liquid.
θ = angle of contact of a liquid with the surface of a capillary bore.
κ = specific conductance of a liquid in a membrane.
$\mu = 10^{-6}$ meter.
$m\mu$ = milli-μ; 10^{-9} meter.
$\pi = 3.1416$.
σ = surface tension of a liquid.
A = cross sectional capillary area.
D = specific inductive capacity (dielectric constant).
d = density of a substance.
E = potential gradient resulting from an applied electromotive force.
F = force.
g = acceleration of gravity.
h = height of rise of a liquid in a capillary.
pH = concentration of hydrogen ions.
I = electric current.
K = a mathematical constant.
l = length of the uniform capillary equivalent to the path of flow of liquid through a wood membrane. For a transverse section of softwood less than a tracheid length in thickness l is equal to the thickness of the membrane.
m = milli, as in $m\mu$.
m = abbreviation for "pit membrane," as in r_m.
N = number of capillaries in a bundle of them.

[1] Received for publication Apr. 11, 1928; issued January, 1929. Portions of the work reported in this paper were communicated to Colloid Symposia and published in abbreviated form in the fourth and sixth Colloid Symposium Monographs (*30, 35*). Since the investigations supply the basis for further studies and are of broad interest in research, the full account of them is here published in combined form.

[2] Reference is made by number (italic) to "Literature cited," p. 66.

P=applied pressure.
O=pressure per unit of area.
q=effective capillary cross section of a wood membrane, or a bundle of uniform capillary tubes.
q_m=effective capillary cross section of the pores in pit membranes.
r=radius of a capillary.
r_m=radius of a pore in a pit membrane.
S=area of one face of a membrane exposed to a liquid (that is, area not masked).
t=average tracheid length.
V=volume rate of flow (of water) through a wood membrane.
x_m=sum of the thickness of all the pit membranes traversed in series by a liquid passing through a wood section more than a tracheid length in thickness.

I. CAPILLARY STRUCTURE AS INDICATED BY ELECTROENDOSMOTIC-FLOW STUDIES

The development of a reliable method for measuring the effective capillary cross section of wood in its different structural directions and after different physical treatments is of considerable importance. By "effective capillary cross section" is meant the cross section of the straight, smooth, circular capillaries that will allow liquid to pass at the same rate, under the same flow conditions, as through the broken system of irregular capillaries actually in the porous material. The determination of this net effective void cross section would be invaluable in theoretical studies of both the seasoning and the preservation of wood, and it might also be of use in the study of the growth processes of the tree. A comparison of the total effective radial capillary cross section of tangential sections with the ray-cell cross sections would show to what extent the radially extending cells of the rays (wood rays) act as continuous capillary tubes. The determination of the effective continuous longitudinal capillary cross section in softwoods free of resin ducts might throw some light on the effectiveness of the pit communication from tracheid (softwood fiber) to tracheid. This effectiveness remains more or less a mystery, although Bailey (*1*, *2*) has shown qualitatively that in some seasoned softwoods there is a continuous longitudinal capillary communication from tracheid to tracheid through the pits (minute openings, with pore-pierced membranes across them, in the tracheid walls) even for colloidal solutions of carbon. Microscopical examinations of softwood sections made by Griffin of the United States Forest Products Laboratory (*17*, *18*) show a general proportionality between the number of pits that are aspirated (closed by the tori) and the resistance to penetration by preservatives. The findings also suggest that fewer pits are aspirated in sapwood than in heartwood, and that seasoning increases aspiration. This points to a more nearly complete capillary system through the sapwood than through the heartwood, as the result of continuous pit communication, and a decrease in capillary effectiveness upon seasoning. Quantitative data in these respects would be of considerable value.

In considering methods of investigation it seemed reasonable to assume that an application to wood membranes of the principle of electroendosmosis (the passage of a liquid through a porous membrane under an electrical potential) might lead to the solution of some of the structural problems mentioned, especially since the relationship among the variables involved has been shown to hold for other colloidal membranes as well as for the simple case of glass capillaries

(*16, p. 240–248; 23*). That principle accordingly formed the working basis of the experiments to be described. Softwoods were chosen for the initial experimental work in preference to hardwoods because of the greater degree of uniformity in their cell structure; the softwood tracheids are free from the large openings that occur in the end walls of the sap-conducting vessels of the hardwoods, and the range in cross-sectional area among the individual cell cavities is less for the softwoods.

THEORY OF ELECTROENDOSMOSIS

The phenomenon of electroendosmosis depends essentially upon the fact that every solid material in contact with a liquid assumes an electrical charge with respect to that liquid. Two distinct potential differences may in general be associated with this charge; the "solution" potential between the solid itself and the bulk liquid, and the "contact" potential between the adsorbed surface layer of ions on the solid and an excess of ions of opposite sign in the adjacent liquid layer. The two layers assumed to exist according to this theory are generally referred to as the "Helmholtz double layer" (*15*). It is the contact potential that is effective in the phenomenon of electroendosmosis. With a fine suspension of solid particles in water, an electrical migration of the particles results as a consequence of the contact potential when an external electromotive force is applied, just as occurs with ions in a solution. If the particles are rigidly held together in the form of a porous membrane, however, no motion of the particles can result, but the liquid, which is of opposite polarity, can and does move relatively to the membrane when a current, no matter how small, flows through the system as a result of the external electromotive force.

The volume rate of passage, V, depends upon the contact potential, ζ, the potential gradient across the membrane resulting from the applied electromotive force, E, the specific inductive capacity (dielectric constant) of the liquid, D, the effective capillary cross section of the membrane, q, and the viscosity of the liquid, η. It may also be expressed in terms of the current flow, I, and the specific conductance of the liquid in the membrane, κ. The relationship is

$$\zeta = (300)^2 \frac{4\pi\eta V}{EDq} = (300)^2 \frac{4\pi\eta V\kappa}{ID} \qquad (1)$$

All the quantities are expressed in centimeter-gram-second units, except that the potential gradient is in volts per centimeter and the current flow in amperes. In the investigation the first form of the fundamental equation was used exclusively; it will be shown later why the second form can not be directly used to determine ζ, even though it does not involve the unknown q.

The factor in equation (1) of chief interest from the standpoint of this investigation is the effective capillary cross section q. For a bundle of smooth, regular capillary tubes of circular cross section, q is equal to the total void cross section. For a naturally porous material like wood and for memberanes built up of fine granular particles, the capillary structure is more complicated. In these cases q represents the net effective continuous capillary or void cross section. The effective capillary cross section will in general be

less than the actual void section in any one plane, owing to irregularity and even discontinuity in the individual capillary systems. It is, however, this effective void cross section that is of interest in all studies of liquid flow in wood.

The validity of the relationships among the various factors in equation (1) has been experimentally confirmed (*15*, *28*), although values of ζ have never been verified by any direct method. By the method of determination to be described later, ζ was found to be a true constant, practically speaking, for the species and under the experimental conditions used. Having determined the value of ζ with sufficient accuracy, values of q in different wood membranes can thereafter be determined simply from measurements of V and E.

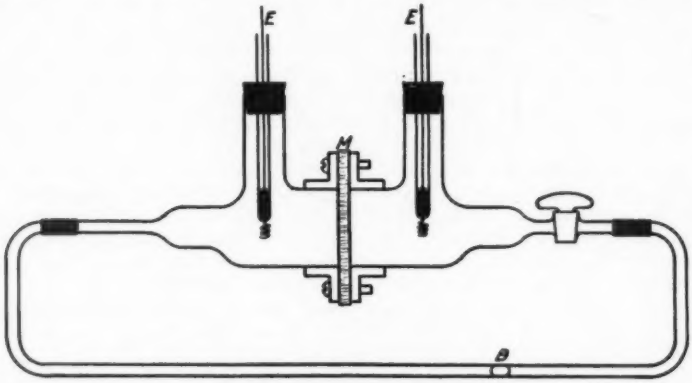

FIG. 1.—Electroendosmosis apparatus

APPARATUS AND METHOD

The apparatus used in this investigation was that of Briggs (*9*) as modified by Strickler and Mathews (*35*) in their studies of the electroendosmosis of nonaqueous solutions. It is illustrated in Figure 1. The membrane, M, was clamped between the brass flange connections, which were fitted with rubber dam gaskets. The apparatus was then filled with distilled water having a conductivity of 5.4×10^{-6} mhos (reciprocal ohms) and a pH of 5.4, the stopcock being manipulated in such a way as to trap a small air bubble, to serve as an indicator, in the (lower) return tube. The platinum-coil electrodes, E, with air-vent slots in the stoppers, were then inserted and an electromotive force of any desired value up to 1,080 volts, supplied by 24 batteries of 45 volts each, was applied between them; a milliammeter indicated the flow of current. The resulting potential gradient across the membrane M caused a flow of the liquid from anode to cathode and produced a corresponding motion of the indicator bubble B. The motion of the bubble was recorded in cubic centimeters per second. A reversing switch in the electrical circuit made it possible to obtain motion of the bubble in either direction. When the apparatus was properly leveled no difference in rate in the two directions was observable. The membrane cross section was 7.76 square centimeters, and the distance between the electrodes was

approximately 6.5 cm. Three different indicating bubble tubes, having cross sections respectively of 0.0251, 0.0550, and 0.0909 square centimeter, were used. Check values for the velocity of liquid flow were obtained with the different tubes except where the velocity was so great that an excess hydrostatic head was built up in one of the necks through which the electrodes were inserted; such a head manifested itself by an appreciable motion of the bubble after the electrical circuit was broken. This head developed chiefly with membranes of high porosity, and with such membranes the largest tube alone was used. The rate of flow was independent of the length of the bubble, which varied from 1.5 to 2 times the diameter of the tube. The apparatus was immersed in a thermostatically controlled water bath held at the constant temperature desired. The rate of motion of the bubble accelerated slightly upon closure of the electrical circuit, so that the rates were determined after the velocity appeared to have become constant.

The drop in potential across each membrane was measured with a potentiometer after measurements of flow were completed. Platinum-black foil electrodes 1 cm. square were clamped securely against the faces of the membrane. A resistance of sufficient magnitude (99,000 ohms) to divert a negligible proportion of the current was connected across them in parallel with the membrane. The potential drop across 2,000 ohms of the resistance was read on the potentiometer and the full electromotive force across the membrane was calculated.

Sections Studied

Transverse, radial, and tangential sections of the following softwoods were studied: Sitka spruce, Alaska cedar, western red cedar, western hemlock, Rocky Mountain Douglas fir, and western yellow pine. These species, containing few if any resin ducts, were chosen to simplify the analysis of the data. All sections were cut with a fine miter saw from clear heartwood of air-dried stock. The sections varied in thickness from 0.04 to 1.45 cm. In the thinner transverse sections most of the tracheids (0.2 to 0.6 cm. long) were cut across twice, so that the effective capillary cross section approached the total cross section of the open cell cavities. Resin ducts, ring shakes, and any tearing action of the saw on the tracheids all tend to increase the effective capillary cross section.

The capillary cross section of the tangential sections is made up largely of the ray-cell sections, plus any effective cross-grain section of resin ducts and tracheids caused by deviations of the cell structure from parallelism with the membrane faces. This increment would be expected to be small, since the length of the tracheids is considerably less than the distance through the membrane at a small angle with its surface, so that any extra flow would have to occur through the obstructed path between successive tracheid ends. Further, the potential gradient is less along this path, giving a correspondingly smaller rate of flow and so diminishing still further the contribution of the path to the virtual void section. Besides these channels of capillary movement, there is the possibility of capillary communication from cell cavity to cell cavity through the occasional pits that occur on the tangential faces of the tracheids, and, finally, there is the possibility of submicroscopic transfusion. Ring shakes at a

small angle with the faces of the sections and checks would also contribute to the effective capillary cross section.

The capillary cross section of the radial sections may be made up of all of the capillary elements of the tangential sections with the exception of the ray-cell cross sections. Perhaps there may also be an increased pit communication caused by the greater number of pits on the radial faces of the tracheids than on the tangential.

All of the sections were soaked in distilled water for at least two weeks. To facilitate the replacement of air by water, the soaking was done in a vacuum desiccator to which suction was applied intermittently.

Direction of Flow

The direction of motion of distilled water through the wood membranes was found to be always from anode to cathode, indicating that wood is negatively charged with respect to pure water, presumably because of its selective adsorption of hydroxylions. Qualitative experiments by Bethe and Toropoff (*6*) gave similar results. The presence of electrolytes has a marked effect upon the velocity and the direction of electroendosmosis, as has been shown by the author in another publication (*32*). In this investigation only distilled water was used.

Test of Electroendosmosis Equation

The validity of the relationships among the essentially variable quantities V, E, q, and η in the electroendosmosis equation was first tested to make sure that they apply to wood membranes, which have definite structural differences in the three directions in space. For this purpose equation (1) may be written in the following form:

$$V = K\frac{Eq}{\eta} \tag{2}$$

in which K, a constant for any given set of conditions, is equal to

$$\frac{\zeta D}{4\pi(300)^2}$$

The linear relationship between the rate of flow V and the potential gradient E was found to hold over the whole range investigated (270 to 1,080 volts applied E. M. F.) for several transverse sections of different thicknesses, the graph showing the relationship being a straight line through the origin.

V was found to vary directly with q. The exposed face area of the membrane, S, was varied by applying brass disk masks coated with shellac to seal the unexposed capillary structure of the membrane. Assuming the structure to be uniform, which may reasonably be allowed, q is the same fractional part of each of the exposed cross sections of the wood; hence, constancy of the ratio $V{:}S$ indicates constancy of $V{:}q$. Table 1 shows the results of this test. Masking the membrane did not appreciably disturb the electrical conditions. The resistance of the membrane was evidently little altered, since E was but slightly affected. The total current remained practically the same after masking, though the part of the current effective in causing electroendosmosis was necessarily reduced in proportion to the decrease in V.

TABLE 1.—*Change in velocity of flow with change in membrane area exposed*

[Wood, heartwood of western red cedar; section, transverse; thickness of membrane, 0.208 cm.]

Velocity of flow V	Exposed face area S	V/S
C. c./sec.	*Sq. cm.*	
0.0647	7.76	0.00833
.0413	5.11	.00809
.0171	2.09	.00818

V was further found to vary inversely as the viscosity η, E remaining practically constant during the test. (See Table 2.) Burton (*10, p. 440*), in cataphoresis studies, obtained temperature-change effects analogous to those recorded in Table 2, an increase in temperature giving an increase in particle velocity corresponding to the decrease in viscosity.

TABLE 2.—*Effect of viscosity on the rate of electroendosmosis through transverse sections of wood*

Species of wood; heartwood only	Thickness of membranes	Temperature	E	V	η	$\eta V \times 10^6$
	Cm.	*° C.*	*Volts/cm.*	*C. c./sec.*	*Poises*	
Alaska cedar	0.135	25	108.7	0.0572	0.00895	5.12
		30	106.7	.0628	.00798	5.03
Western hemlock	.160	25	110.0	.0697	.00895	6.23
		30		.0767	.00798	6.13

VELOCITY OF ELECTROENDOSMOSIS AND POTENTIAL-GRADIENT DETERMINATIONS FOR THIN SECTIONS

The preceding experimental verifications of the direct proportionality between V and E and between V and q and of the inverse proportionality between V and η substantiate the general relationship of equation (1) sufficiently well for the purpose of this investigation. Variations of electroendosmotic velocity V and potential gradient E under an applied electromotive force of 1,080 volts in some thin membranes of different species of wood, cut in different directions of grain, will now be discussed for their general interest and their bearing on the remainder of the investigation. The data to be considered are shown in Table 3.

The rate of endosmosis through the transverse sections as a rule decreases with an increase in thickness of section, presumably because of the corresponding decrease in the proportion of the open-cell cavities that extend over the entire thickness of the membrane. There are one or two exceptions to the rule, but the variation is in no case pronounced, since the sections are all of the same order of thickness. This effect, which is of primary importance, is given special attention later. The data for Sitka spruce suggest that different velocities of electroendosmosis will be obtained for sections taken from wood of the same kind but of different densities, the denser wood giving the smaller rate of flow, as would be expected. For the sections studied, the rate of endosmosis is 10 to 100 times as great through the transverse sections as through the tangential sections and 3 to 12 times as great through the tangential sections as through the radial.

TABLE 3.—*Electroendosmosis measurements on thin wood membranes at 25° C. and 1,080 volts applied electromotive force*

[Data within braces apply to adjacent sections]

Species of wood; heartwood only	Direction of cutting	Thickness of membrane	*V*	*E*	Density of wood
		Cm.	*C. c./sec.*	*Volts/cm.*	
Sitka spruce	Transverse	0.117	0.0712		0.304
Do	do	.157	.0693		.304
Do	do	.109	.0552	107.3	.408
Do	do	.150	.0563	110.3	.408
Do	Tangential [a]	.043	.00575		.408
Do	do	.053	.00365		.408
Do	do	.056	.00424	275	.408
Do	do	.061	.00453	272	.408
Do	Radial	.114	.00035	254	.408
Do	do	.117	.00033	260	.408
Alaska cedar	Transverse	.117	.0587		.442
Do	do	.135	.0572		.442
Do	do	.137	.0572	108.7	.442
Do	do	.186	.0547	107.1	.442
Do	Tangential	.043	.00148	241	.442
Do	do	.048	.00137	245	.442
Do	Radial	.119	.00023	222	.442
Western red cedar	Transverse	.152	.0676	106	.290
Do	do	.208	.0576	106.8	.290
Do	Tangential	.048	.00090	227	.290
Do	do	.076	.00080	224	.290
Do	Radial	.054	.00021	215	.290
Do	do	.089	.00023	218	.290
Western hemlock	Transverse	.127	.0707	105	.343
Do	do	.130	.0707	104	.343
Do	do	.160	.0697	110	.343
Do	Tangential	.058	.00160	264	.343
Do	do	.085	.00144	256	.343
Do	Radial	.122	.00033		.343
Do	do	.122	.00029		.343
Douglas fir (Rocky Mountain type)	Transverse	.099	.0558	108	.526
Do	do	.125	.0543	109.3	.526
Do	Tangential	.084	.00058	237	.526
Do	do	.091	.00044	244	.526
Do	Radial	.132	.00017		.526
Western yellow pine [b]	Transverse	.114	.0621		.466
Do	do	.132	.0602		.466
Do	do	.157	.0585		.466
Do	Tangential	.068	.00111		.466
Do	do	.112	.00090		.466
Do	do	.127	.00080		.466
Do	Radial	.076	.00030		.466
Do	do	.122	.00029		.466

[a] Slight visible check.
[b] Temperature of water bath for these specimens was 30° C. Values for *V* have been corrected to 25° C.

For all the species studied, the potential gradient across sections cut in a given structural direction was found to be practically constant, although it varied with the direction of cutting. In general, the gradients across the tangential sections were more than twice as great as those across the transverse sections. The difference between gradients across radial and tangential sections was less pronounced. Since the current was practically constant for the thin sections, the same proportionality holding between potential gradients holds for the specific resistances of different sections. The specific resistances of sections with moisture-content values below the fiber-saturation point have been found, similarly, to be about twice (1.5 to 2.5 times) as great for radial and tangential as for transverse sections. It has been shown that the actual values of the electrical resistance of wood change but slightly above the fiber-saturation point but increase very rapidly with a decrease in moisture content below that point (*22*, *31*). These facts, together with the observation just made, that the ratios

of the resistances in the different structural directions above and below the fiber-saturation point are roughly equal, are strong indications that electrical conduction in wood is an internal surface phenomenon.

CONDUCTIVITY OF WATER IN THE MEMBRANE AS RELATED TO THE CALCULATION OF ζ

Further, the conductivity of water in the membrane is greater than that of water in bulk. The conductivity of the water used in these experiments was 5.4×10^{-6} mhos (reciprocal ohms) and that of the average soaked transverse section of Sitka spruce, as determined by the potential gradient and current flow measurements, 8.3×10^{-6} mhos. Since the average volume of water in a soaked section of this wood is about 74 per cent of the total wood-water volume,[3] the conductivity of water in the membrane, assuming the wood substance itself to be nonconductive, is seen to be $8.3 \times 10^{-6} \div 0.74$, or 11.2×10^{-6} mhos, which is a little more than twice that of the water in bulk. A similar increase in the conductivity of water and of dilute solutions has been observed by Stock (*34*) in powdered quartz and by McBain (*26*) in silica capillaries. The increased conductivity is believed to be due to a higher conductivity of the more definitely arranged hydrogen and hydroxyl ions of the water at the solid-liquid interface as a result of the selective adsorption of the hydroxyl ions (*16, p. 240–248; 23*). It is on account of this increased conductivity of the liquid in the membrane that the contact potential ζ can not be calculated directly from the second form of equation (1). Although the equation does not involve the unknown q directly, q must be known in order to determine κ (*16, p. 240–248; 23*). Fairbrother and Mastin (*14*) have determined $\frac{q}{l}$ independently by conductivity measurements on membranes of carborundum powders, where l is the thickness of the section. Using salt solutions of sufficiently high concentrations so that the specific conductance of the solutions in bulk and in the membrane were supposedly the same, and assuming the conductivity of the membrane material itself to be negligible, these investigators calculated $\frac{q}{l}$ by dividing the specific conductance of the combined membrane-salt solution system by the specific conductance of the solution. Their method may give a satisfactory determination of effective capillary cross section for substances in which there are presumably no structural differences in the three directions in space and all of the liquid in the membrane is in such a state of dispersion as to permit not only electrical conduction but electroendosmotic flow as well. These conditions do not necessarily hold for wood membranes in which part of the water may be held in a state of dispersion as fine perhaps as molecular. In other words, it is conceivable that water in molecular dispersion may be effective in electrical conduction and still not be subject to electroendosmotic motion because of the absence of a complete Helmholtz double layer. Thus the effective capillary cross section of the wood membrane for electrical conductance need

[3] Density of Sitka spruce in C. G. S. units, based on weight when dry and volume when wet, 0.40; density of wood substance, 1.55; volume of water, $1 - \frac{0.40}{1.55} = 0.74$.

not be the same as for electroendosmotic motion. Such is very probably the case, since the ratio of the effective *conductance* cross section in a longitudinal direction through thin wood sections to that in a transverse direction, from the preceding potential gradient data, is about two to one, whereas the effective *capillary* flow cross section is known to be of the order of 100 times as great longitudinally as transversely. Accordingly a different method of determining both q and ζ was tried.

DETERMINATION OF CONTACT POTENTIAL ζ

A number of holes of capillary size, varying in diameter from 0.044 cm. to 0.0913 cm., were drilled in soaked tangential and radial sections, and the increase in the rate of electroendosmosis after drilling was determined. Over the range studied the increase in rate of endosmosis, ΔV, was found to be strictly proportional to the artificial increase in capillary cross section, Δq. Further, no change was detected in E after the holes were drilled. It therefore seemed quite justifiable to set up as a basis for calculation the equation

$$\zeta = (300)^2 \frac{4\pi\eta}{ED} \frac{\Delta V}{\Delta q}, \qquad (3)$$

which, mathematically, is directly deducible from equation (1). Table 4 gives the values of Δq and ΔV for holes of different sizes and the corresponding calculated values of the contact potential ζ for wood in contact with distilled water. The contact potential varies but slightly among the species studied. The accuracy of the value of ζ is perhaps not better than 10 per cent, even though most of the readings fall well within that variation. Among the reasons for the slight inaccuracy is the possibility of distortion of the holes caused by the release of existing stresses in the sections. This effect should not be great, however, in the saturated sections. A slight tearing effect on drilling, which is unavoidable, would also introduce an error of greater or less magnitude in the calculation of ζ. It should be noted, however, that the average potential of wood against water as thus determined (0.0136 volt) is quite comparable to the value (0.0157 volt) obtained by Harrison (*20*, *21*) for the potential of cotton cellulose against distilled water by streaming potential measurements.

TABLE 4.—*The contact potential of wood with respect to distilled water*

Species of wood; heartwood only	Direction of cutting	Diameter of holes	Number of holes	Δq	ΔV	E	ζ
		Cm.		*Sq. cm.*	*C. c. /sec.*	*Volts/cm.*	*Volt*
Sitka spruce	Tangential	0.0635	25	0.0790	0.00235	273	0.0136
Do	Radial	.0635	50	.1580	.00478	263	.0144
Alaska cedar	Tangential	.0444	70	.1085	.00272	224	.0140
Do	do	.0520	70	.1482	.00350		.0132
Do	do	.0648	50	.1650	.00392		.0133
Do	do	.0780	50	.2390	.00562		.0131
Do	Radial	.0610	50	.1464	.00358	222	.0138
Western red cedar	Tangential	.0635	50	.1580	.00380	224	.0134
Do	Radial	.0635	50	.1580	.00387	215	.0142
Western hemlock	Tangential	.0610	50	.1464	.00418	264	.0134
Douglas fir (Rocky Mountain type.)	do	.0610	50	.1464	.00366	237	.0132

DETERMINATION OF EFFECTIVE CAPILLARY CROSS SECTION q FOR THIN SECTIONS

The value of the contact potential ζ having been determined, the value of the effective capillary cross section q for any membrane can be calculated from flow and potential-gradient measurements by means of the first form of equation (1). The effective longitudinal capillary cross section thus determined for a number of thin transverse wood sections is shown in Table 5 as a percentage of the total membrane area. Over against this percentage is shown the maximum total percentage void area calculated from the density of the wood. The latter is the ideal capillary cross section, supposing all the cell cavities to be open at both ends and the volume of independent capillary systems in the radial and the tangential directions to be a negligible proportion of the total void volume. The percentage void volume (or ideal percentage void area in the case of a membrane) is equal to $100\left(1-\frac{d}{d_o}\right)$ where d is the virtual density of wood as a body and d_o the real density of the actual wood substance, which is 1.55 (gm./c. c.) by water displacement. The effective capillary cross sections calculated for these transverse membranes from the electroendosmosis measurements approach the ideal values, though they would of course never be expected to be quite equal to them because some of the tracheids will always terminate in a section regardless of how thin it is, and because independent ray-cell systems are present. The proximity of the two values, however, does serve excellently as a check on the magnitude of the calculated values of the contact potential ζ.

TABLE 5.—*Effective capillary cross section of transverse sections of wood*

Species of wood; heartwood only	V at 25° C.	Thickness of section	Density of wood	q (in percentage of total membrane area)	Ideal capillary cross section (in percentage of total membrane area, from density)
	C. c./sec.	*Cm.*			
Sitka spruce	0.0712	0.117	0.304	76.5	80.4
Do	.0674	.110	.370	72.6	76.1
Do	.0563	.150	.408	60.5	73.7
Alaska cedar	.0572	.137	.442	61.7	71.5
Do	.0577	.115	.508	63.6	67.3
Western red cedar	.0676	.152	.290	73.3	81.3
Western hemlock	.0707	.127	.343	75.2	77.9
Douglas fir (Rocky Mountain type)	.0543	.125	.526	54.8	66.1
Western yellow pine	.0622	.114	.410	62.8	73.6

Table 6 shows the effective void area of tangential sections calculated from electroendosmosis measurements, expressed as percentages of total membrane area, and, for comparison, the total void cross section of the ray cells in a few membranes (calculated on the same percentage basis) as determined from photomicrographs[4] by the method of cutting out and weighing the ray-cavity sections. Values in the two columns, as far as shown, check fairly closely, although in two or three cases q is in excess. The total void cross section of the ray

[4] For the photomicrographic work the author is indebted to A. I. Weinstein, of the United States Forest Products Laboratory.

cells may be expected to exceed somewhat the effective capillary cross section, since all the rays may not act as continuous tubes even for the thin sections listed. Indications of such discontinuity in fact appear in Table 3, which tends to show a slight increase in V for decreased thickness of adjacent tangential sections. While such an effect might be operative and might be compensated or overbalanced, as in the cases alluded to by the capillary area of pits and by any possible checks, it is nevertheless believed that the principal void area of tangential sections is that of the ray cells.

TABLE 6.—*Effective capillary cross section of tangential sections of wood*

Species of wood; heartwood only	V at 25° C.	Thickness of section	q (in percentage of total membrane area)	Void area of ray cells (in percentage of total membrane area)
	C. c./sec.	*Cm.*		
Sitka spruce	0.00453	0.061	1.97	1.19–1.90
Do	.00424	.056	1.84	
Do	.00365	.053	1.59	
Alaska cedar	.00148	.043	.73	0.79
Do	.00137	.048	.67	
Western red cedar	.00080	.076	.41	.39
Do	.00090	.048	.46	
Western hemlock	.00160	.058	.75	.82
Do	.00144	.085	.68	
Douglas fir (Rocky Mountain type)	.00058	.084	.30	.26
Do	.00044	.091	.22	
Western yellow pine	.00112	.068	.58	
Do	.00090	.112	.46	

The calculated effective capillary cross section of radial sections in percentage of total membrane area is shown in Table 7. The values, which are small, are very likely due almost entirely to pit communication. If such is the case, the values given are of course smaller than the *actual* area of openings in the pit membranes, since the path of flow of the liquid from tracheid to tracheid through the pits in a tangential direction is doubtless several times the straight path across the section. Thus the effective potential gradient across the sections would be less than that calculated and the actual open area correspondingly larger.

TABLE 7.—*Effective capillary cross section of radial sections of wood*

Species of wood; heartwood only	V at 25° C.	Thickness of section	q (in percentage of total membrane area)
	C. c./sec.	*Cm.*	
Sitka spruce	0.00035	0.114	0.16
Do	.00033	.117	.15
Alaska cedar	.00023	.119	.12
Western red cedar	.00021	.054	.11
Do	.00023	.089	.12
Western hemlock	.00033	.122	.17
Do	.00029	.122	.15
Douglas fir (Rocky Mountain type)	.00017	.132	.09
Western yellow pine	.00030	.076	.16
Do	.00029	.122	.15

EFFECT OF THICKNESS OF TRANSVERSE SECTION

The effect on the rate of endosmosis of a considerable range of thickness of transverse sections of all the species studied was determined. The results of the experiments, made at 30° C. with a potential gradient of 105 to 110 volts per centimeter, are shown in Figures 2, 3, and 4. The velocity for a hypothetical zero thickness was calculated as for a section having the ideal void area determined

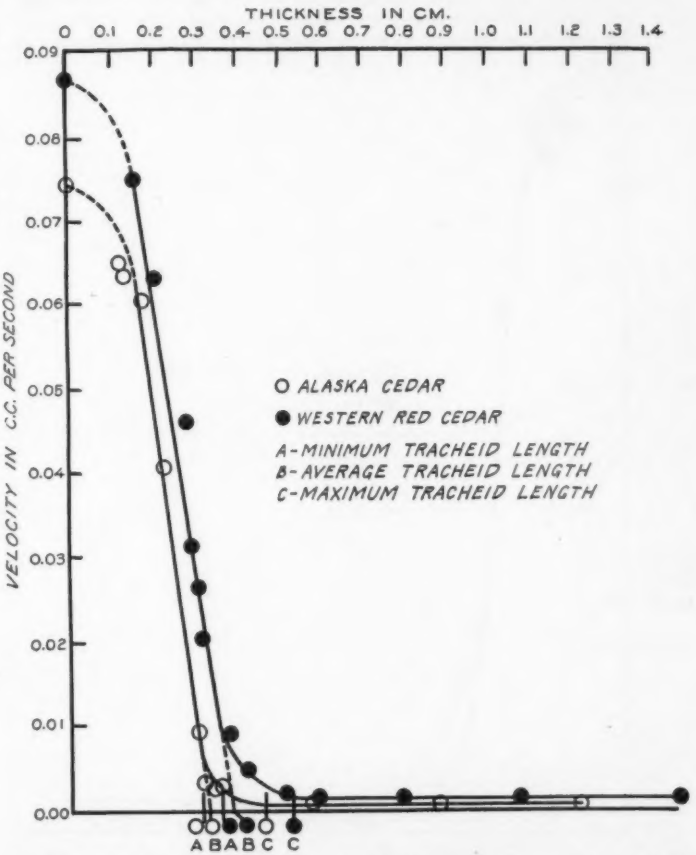

FIG. 2.—Change in velocity of electroendosmosis with thickness of transverse sections, for heartwood of Alaska cedar and of western red cedar

by the specific gravity of the wood, as previously explained, assuming E to remain constant. The rate of electroendosmosis decreases rapidly for an increase of the thickness of the sections up to a value which is about the average tracheid length. Beyond that point it decreases more slowly, and finally becomes constant for a thickness greater than that which may be taken to represent the maximum tracheid length.

Analysis of Curves

A brief consideration of the nature of these curves seems necessary to bring out their significance. Let us first suppose that the wood is made up of uniform closed tubes of equal length with no voids between either adjoining ends or adjoining outer walls, and that the position of these tubes with respect to one another in the longitudinal direction

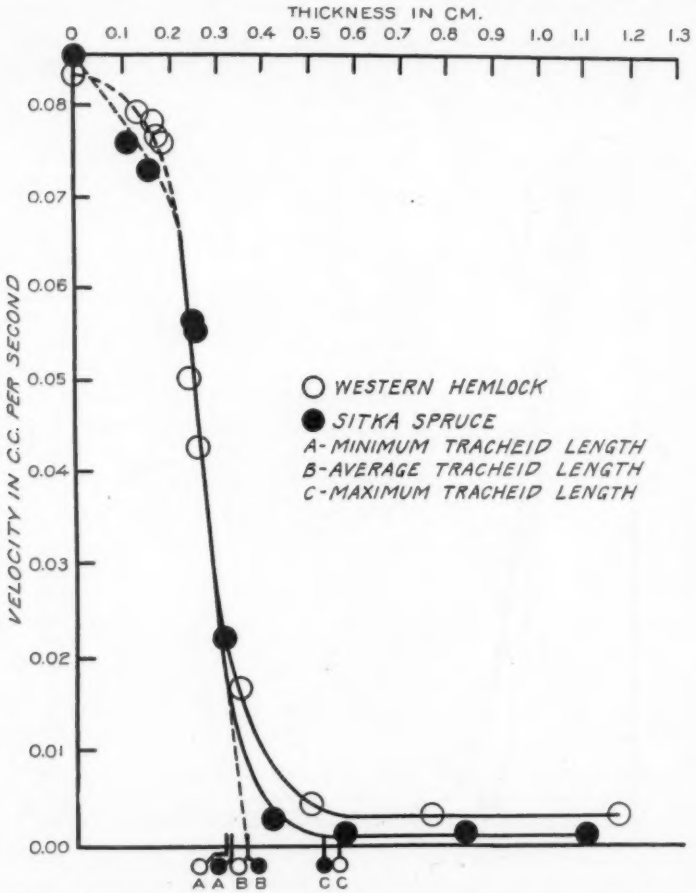

Fig. 3.—Change in velocity of electroendosmosis with thickness of transverse sections, for heartwood of western hemlock and of Sitka spruce

is perfectly arbitrary except that the arrangement is statistically uniform for as large a number of tubes as there are tracheids in the experimental sections. The proportion of tubes that have one end falling within any section cut across the bundle will thus vary directly as the thickness of the section, a straight-line relationship. The open area of cross section will vary from the total open cross section of the

tubes, in the case of infinitesimally thin sections, to zero in the case of sections having a thickness equal to the tube length. When the tubes have a different length from that first assumed, a similar straight-line relationship will hold between the total open cross section and the thickness of the section, but the slope of the line will be different. All lines will have a common point for zero thickness of section, but each will have a different terminal point corresponding

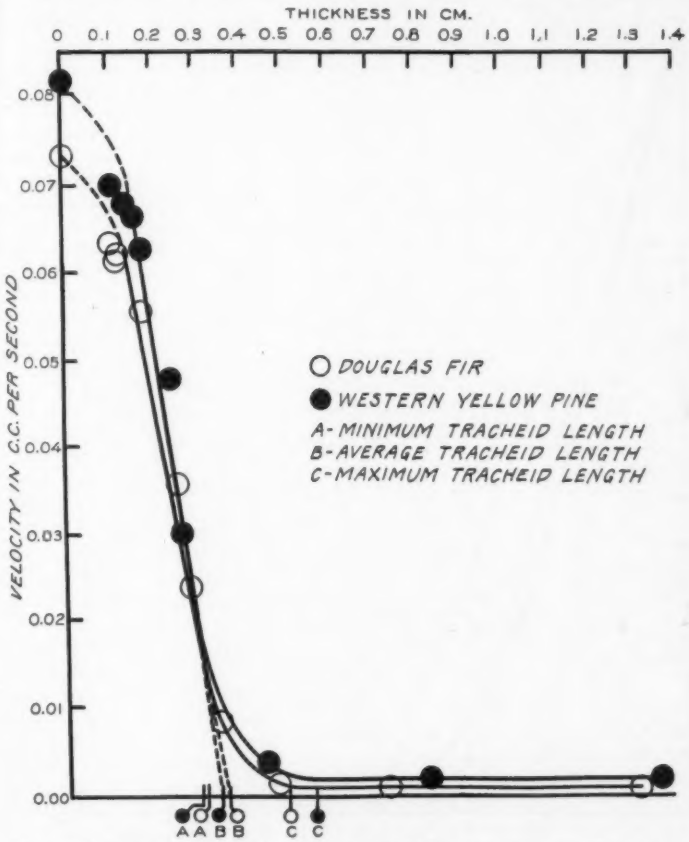

FIG. 4.—Change in velocity of electroendosmosis with thickness of transverse sections, for heartwood of Douglas fir and of western yellow pine

to the tracheid length. The dotted lines (2, 3, and 4) in Figure 5 represent the fractional change in open tube cross section with changes in thickness of the section for cylinder lengths of 2, 3, and 4 units. If, now, equal numbers of each of these three lengths of cylinders are mixed in a single bundle of the same size, the *solid compound line*, D, will result, the ordinates of which represent average values of the open capillary cross sections corresponding to the respective section thicknesses for the three different tube lengths.

In any softwood the tracheid lengths vary between definite limits. Presumably the deviations from the most probable length will follow a form of the Gaussian distribution law and in most cases will be only slight. Such facts tend to cause the line representing the proportional change of open area with respect to membrane thickness to curve off gradually to the right as the tracheid lengths are exceeded by the thickness in a manner dependent upon the nature of the distribution of tracheid lengths, rather than to take the form of a series of broken lines.

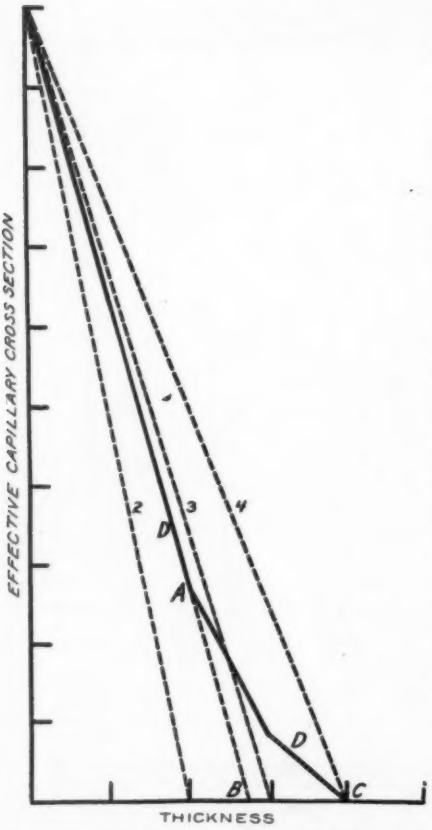

FIG. 5.—Theoretical change in effective capillary cross section with change in thickness of wood membrane

TRACHEID LENGTHS

The point where the average straight line just mentioned starts to curve to the right (A in the hypothetical case represented in fig. 5) corresponds to the minimum tracheid length, the curvature being due to the elimination of tracheid-length classes. The point where the curve intersects the axis of abscissas, or, as in the actual case of a wood membrane, becomes parallel to it, corresponds to the maximum tracheid length (cf. C, fig. 5). The point, B, Figure 5, where the continuation of the straight line through A intersects the axis of abscissas (or the continuation of the limiting horizontal straight line in the case of actual wood) will approach the point corresponding to the average tracheid length as the deviation of individual tracheid lengths from the mean becomes smaller and smaller. The deviation from the average tracheid length in the experimental sections may safely be assumed to be much less than in the hypothetical case because of the smaller mean deviation in the distribution of tracheid lengths.

Table 8 gives some statistics on tracheid lengths collected by the United States Forest Products Laboratory and corresponding values obtained from electroendosmotic-flow graphs (as indicated). The agreement is interesting, considering that the measurements were not made on the same specimens.

TABLE 8.—*Tracheid lengths*

Species of wood	Direct measurement				Measurement by electro-endosmosis		
	Number measured	Minimum	Average	Maximum	Minimum	Average	Maximum
		Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
Sitka spruce		0.23	0.28	0.37			
Do	50	.24	.42	.54	0.32	0.38	0.52
Do	50	.18	.36	.51			
Do	50	.24	.41	.54			
Alaska cedar					.31	.35	.46
Western red cedar		.31	.38	.45	.33	.38	.53
Western hemlock		.18	.31	.37	.31	.38	.55
Douglas fir	900		.32		.32	.38	.50
Western yellow pine					.30	.35	.57

The tracheids do not all have the same lumen (cell cavity) cross section, as was assumed in the hypothetical case, but may differ by as much as sixfold. There is a slight tendency for the summerwood tracheids, which have a smaller cross section of lumen, to be also somewhat shorter; the average tracheid length of the summer wood of some softwoods is about 20 per cent less than that of the corresponding spring wood. This means that the straight lines representing the change of open section with membrane thickness for different tracheid-length classes will not have the same point in common for membranes of infinitesimal thickness. The result of this disparity of lumen area of tracheids in a single membrane, however, would be merely a vertical shift of the point representing maximum open area of section; it would not cause the line representing change of total open area with thickness to curve to the left at the upper end, as the experimental graphs do. (Figs. 2, 3, and 4.)

Examination of the curvature of the experimentally determined graphs brings out some interesting possibilities. The hypothetical analogue takes no account of any slight capillary communication from tube to tube, which would correspond to the continuous pit communication in actual wood. Superimposing this effect upon that already considered may account for part, at least, of the deviation of the actual measurements from the hypothetical case. This is definitely a fact for the thicker sections. The graphs all become parallel to the length axis beyond the maximum tracheid length, showing that there is a continuous and uniform residual open section for every kind of wood tested. The effective section presumably can be made up only of resin ducts, pit openings between tracheids, and open area caused by such defects as checking. Microscopical examination of the thicker sections showed appreciable checks only in western hemlock. In Alaska cedar and western red cedar there are no resin ducts. Therefore their residual open areas, shown in Table 9, must represent that of the pit openings alone. Effective pit-communication areas for the other species were obtained by subtracting the values determined microscopically for the resin-duct sections from the total continuous open section.

TABLE 9.—*Continuous effective open area of transverse sections*

Species of wood; heartwood only	V at 30° C.	q (in percentage of total membrane area)	Resin duct cross section (in percentage of total membrane area)	Corrected percentage pit-communication cross section
	C. c./sec.			
Sitka spruce	0.00081	0.78	0.04	0.74
Alaska cedar	.00035	.35	None.	.35
Western red cedar	.00053	.52	None.	.52
Western hemlock	.00292	3.00	(1)	
Douglas fir (Rocky Mountain type)	.00033	.33	.03	.30
Western yellow pine	.00129	1.30	.54	.76

[1] A number of radial checks.

The "effective section" mentioned in the preceding paragraph may include submicroscopic openings between tracheids other than those in the pit membranes. The work of Bailey (*1*, *2*) shows that it probably does not; in his studies india ink that penetrated a tracheid wall appeared first, if not entirely, in the pit cavities, indicating that the only natural channel of direct communication from tracheid to adjoining tracheid is through the pit membranes. The later work of the author (Pt. III of this paper, the section headed "Permeability of wood to colloidal solutions," especially the last paragraph) shows that if openings other than those in the pit membranes do occur they are relatively so fine that they have little if any influence on the determination of pit-pore dimensions. Further, taking the length of channel between adjoining tracheids as the probable thickness of the pit membrane, which is assumed approximately equal to that of the middle lamella, gives results comparable to the values secured by the author through other means (see Pt. II, Effect of appreciable changes in thickness), whereas using the full thickness of the tracheid wall instead of that of the pit membrane would cause the results to differ from the values obtained through other methods by amounts so great that the use of the wall thickness would unquestionably be in error. In addition, the work of Scarth (*29*), published after the completion of the present paper, tends to show that the intertracheid flow under discussion is confined to the pores in the pit membranes. Finally, as far as the writer is aware, no theory to account for direct intertracheid flow by natural means other than the pit-membrane pores has ever been advanced. For the purpose of this paper, therefore, the confinement to the pit pores of direct intertracheid flow through natural channels will be considered as established, and statements dependent upon such establishment will be made without the qualification that would otherwise be necessary.

For the thin sections the deviation of the experimental curves from the hypothetical case is more difficult to explain definitely. Three possible causes of the curvature readily present themselves, part or all of which may be effective. In the first place, the velocity of electroendosmotic flow for the hypothetical zero thickness of membrane is a calculated value depending for its correctness upon the constancy of the relationships expressed by equation (1) for infinitesimal as well as for experimental thicknesses of membrane. This constancy need not necessarily be fact. Further, there is the

possibility of this curvature being due to local irregularity in the potential gradient across the sections, which would manifest itself to a maximum extent in the thin sections. In addition, there is the possibility of an experimental discrepancy caused by the tearing out of tracheids in the process of cutting the thinner sections; the tearing would tend to give too high values for the velocity of electroendosmosis. Such values would account for the break in the curve when extending it from the experimental points to the calculated zero thickness. The tearing effect was actually noticeable in some of the thinnest sections. The evaluation of the relative importance of these different possible causes seems unnecessary, however, for the nature of the curves at this end has no theoretical bearing upon the conclusions drawn or upon the calculations made.

PIT OPENINGS

From the data assembled it is interesting to calculate the probable effective cross section of pit openings. Western red cedar, which has, roughly, an average lumen cross section of 3×10^{-6} sq. cm., may be taken as an example. The total effective capillary cross section is reduced from 73.3 per cent of the membrane area to 0.52 per cent by increasing the thickness of the section beyond that of a tracheid length. That is to say, this reduction takes place when each tracheid is changed from an open tube to one whose effective open area depends upon that of the pits. Hence the effective open area for one-half the pits in a tracheid is about 2×10^{-8} sq. cm. $\left[\text{the calculation is } \frac{(3 \times 10^{-6} \times 0.52)}{73.3}\right]$, half the pits serving to carry liquid into the lumen and half serving to discharge it.[5] Assume that there are, on an average, 100 pits on a tracheid and that 30 of these are not aspirated.[6] This gives 0.13×10^{-8} sq. cm. as the total effective open area of each pit. The pit-membrane openings are very likely made up of a number of considerably smaller pores or voids, so that the diameter of a single pore must be considerably less than 0.4×10^{-4} cm., which would be the diameter for a single opening equivalent to the total open area of each pit.

The effective pit-communication areas of the western yellow pine and Sitka spruce specimens (Table 9) are about three times that of the Rocky Mountain Douglas fir. Assuming the same average number of pits, having openings of the same size, on a tracheid of each species, these figures would indicate that three times as many normal (unaspirated) pits occur on the tracheids of pine and spruce as on those of Rocky Mountain Douglas fir. This is very close to the average value obtained from the tables of Griffin (*17*, *18*) for the ratio of the percentage of effective pits on the tracheids of woods fairly readily treated and woods treated with difficulty (coast Douglas fir 40 per cent, larch 47 per cent, and Rocky Mountain Douglas fir 14.6 per cent).

[5] The assumption on which this calculation is based is that the *effective* capillary section is practically the *minimum* section when great disparity exists between parts of the path. For support of this assumption see Part II of this paper, especially the text under the heading "Effect of appreciable changes in thickness."

[6] Griffin (*17*, *18*) has shown that the proportion of pits that are not aspirated ranges from 2 per cent in the case of practically impermeable specimens of air-dried Rocky Mountain Douglas fir to 50 per cent in the case of air-dried coast Douglas fir and larch, which are fairly readily treated with preservative.

LIMITATIONS OF THE ELECTROENDOSMOSIS METHOD

The method here set forth for studying the capillary structure of a porous material gives only the total effective open section under the various experimental conditions. It reveals directly nothing about the distribution of the capillaries or their variation in size. Consequently, further permeability experiments were undertaken, using other methods of attack; the results appear in Parts II and III of this report.

SUMMARY OF PART I

The capillary structure of several softwoods has been studied from the standpoint of electroendosmotic flow. A comparison of the total capillary cross sections of several conifers shows that the effective lumen (cell cavity) cross section of thin transverse sections approaches the ideal value of the open area calculated from the density of the wood. The effective capillary cross section drops off rapidly as the thickness of the sections increases, since more and more of the tracheids terminate in the section. When a thickness corresponding to the maximum tracheid length is reached a residual continuous open section is found, representing the resin-duct and pit-communication cross sections. Maximum, minimum, and average tracheid lengths obtained from graphs of electroendosmotic flow correspond closely to microscopically measured values.

The effective open capillary section of tangential sections of softwood seems to be almost entirely that of the ray cells; this is indicated by the proximity of the values to the internal ray-cell cross sections obtained microscopically, although the small proportion of the pits on tangential faces may contribute somewhat to the flow.

The calculated effective open area of radial sections seems to be due chiefly to pit communication. It is quite small—three to five times as small as the effective continuous pit communication area in the longitudinal direction. The probable explanation is that the flow in radial sections follows a considerably longer path and traverses a greater number of pits in series than in transverse sections, the *effective* open area being reduced accordingly.

The values for the residual longitudinal flow as a result of pit communication correspond closely to the readiness with which the various species take up preservatives. Rocky Mountain Douglas fir, which is almost impossible to treat, shows the least residual flow. Western yellow pine and Sitka spruce, which can be treated fairly readily, show considerably more. The parallelism between residual flow and a normal condition (nonaspiration) of the pits is also noteworthy.

This investigation has involved a determination of the contact potential between wood and water, which seems to vary but slightly among the species examined. The results also suggest clearly that the electrical conductivity of wood saturated with water is a surface phenomenon.

II. CAPILLARY STRUCTURE AS INDICATED BY HYDROSTATIC-FLOW STUDIES

In capillary flow of liquids under hydrostatic pressure the velocity is dependent not only upon the total effective capillary cross section but also upon the size of the individual ducts. By combining the

data from the electroendosmotic-flow and from hydrostatic-flow studies it becomes possible to calculate the actual size of the average capillary openings and to draw conclusions regarding the structure that determines the effective continuous capillary communication in softwoods. The identical air-dry softwood membranes of the electroendosmosis experiments were used again in hydrostatic-flow studies, so that the effective capillary sizes could be determined.

POISEUILLE'S LAW

The passage of liquids under external pressure through a smooth capillary tube of circular section for conditions of stream-line flow may be quantitatively expressed by Poiseuille's law,

$$V = \frac{\pi r^4 P}{8\eta l} = \frac{A r^2 P}{8\eta l} \tag{4}$$

in which V represents the rate of flow, r the capillary radius, l the capillary length, P the applied pressure, η the viscosity, and A the cross-sectional capillary area, all in centimeter-gram-second units. The equation has been experimentally verified by Osborne Reynolds (*27*) for velocities below the critical value. High velocity of flow, large radius of the capillary, and short length all tend to cause turbulent flow through the tube, a condition that results in deviation from the relationship of this law. Herschel (*24, p. 729*) states that such internal turbulence will probably be negligible when $\frac{rV}{\eta} < 1{,}000$. The impact turbulence occurring at the ends of the tubes, however, must be taken into account and will be considered later.

For a bundle of N capillaries having a total effective capillary cross section q and an average effective individual radius r, which, more strictly speaking, is the fourth root of the average of the fourth powers of the radii,

$$V = \frac{N\pi r^4 P}{8\eta l} = \frac{q r^2 P}{8\eta l} \tag{5}$$

If there is a statistically large number of capillary tubes making up the bundle, with the deviations in cross section from the most probable value following a form of Gaussian distribution law and with most of the cross sections deviating but slightly from the most probable value, r will not differ appreciably from the true average radius. This is the case for the open lumen (cell cavity) capillaries of thin transverse sections of softwood; it thus becomes possible to determine approximately the average effective lumen cross sections and the diameters for the lumina, open at both ends, that make up a thin transverse section, provided that q, the total effective capillary cross section, is known. Since q for each of the sections used was determined in the electroendosmosis investigation previously reported, r can be calculated by combining the value of q with the hydrostatic-flow data.

Differential Method

Instead of determining the volume of discharge of water from the capillary system per unit of time when subjected to a definite head, with the system held at a constant temperature so that η is both de-

terminable and constant, a differential method, which involves several special features, can be used. If the membrane under test and a calibrated capillary tube are connected in series, with the following relations holding:

$$V_1 = \frac{q_1 r_1^2 P_1}{8\eta l_1} \qquad \text{for a wood membrane} \quad (6)$$

$$V_2 = \frac{\pi r_2^4 P_2}{8\eta l_2} \qquad \left\{\begin{array}{l}\text{for a calibrated stand-}\\ \text{ard capillary tube}\end{array}\right\} \quad (7)$$

then, since $V_1 = V_2$ (8)

because of the nature of the system,

$$\frac{\pi r_2^4 P_2}{l_2} = \frac{q_1 r_1^2 P_1}{l_1} \quad (9)$$

Solving for r_1,

$$r_1 = \sqrt{\frac{\pi r_2^4 l_1 P_2}{q_1 l_2 P_1}} \quad (10)$$

This method of making the measurements, besides the obvious advantage of not requiring the system to be placed under thermostatic control, has the important advantage of making the attainment of equilibrium conditions easily determinable. Instead of carrying out a series of measurements of V_1 for each set of experimental conditions, it merely becomes necessary to observe that the ratio $\frac{P_2}{P_1}$ has become constant.

Previous Applications of Poiseuille's Law

Previous applications of Poiseuille's law for the determinations of the dimensions of the capillary openings in natural and in artificial membranes are rather limited. This situation comes from the fact that neither N, the number of capillaries making up each membrane, nor q, the total effective capillary cross section, is readily obtainable. It is true that the average total capillary cross section in any plane cutting a membrane transversely can be calculated by dividing the void volume of the membrane by its thickness, since the fractional void volume is equal to $\left(1 - \frac{d}{d_o}\right)$, where d is the virtual density of the wood as a body and d_o is the real density of the wood substance itself. The average total capillary cross section, however, may differ considerably from the effective total value, or, using the average total in the calculation, the resulting effective length of the path may differ considerably from the actual thickness of the membrane.

Guerout (*19*), making the simplifying assumption that the capillaries are prismatic tubes extending entirely through the membrane, was able to calculate the pore sizes of several natural and artificial membranes. Bigelow (*7*) showed the applicability of Poiseuille's law to goldbeater's skin, parchment paper, and porcelain membranes by proving that V is practically proportional to P over a large range of pressures (1 to 80 cm. of mercury) and is inversely proportional to

the variations of η caused by change in temperature. He was unable to obtain actual values of the capillary dimensions, however, because the effective value of l was indeterminable. Duclaux and Errera (*11*), using the method of Guerout, obtained the pore diameters for cellulose acetate membranes. Hitchcock (*25*) obtained the fractional pore volume of collodion membranes by means of density measurements and also by electrical conductivity measurements. In the electrical procedure he determined the conductivity of a one-fiftieth normal concentration of potassium chloride solution in bulk and again when absorbed in the membrane. Assuming that the observed change in conductivity was entirely due to the change in volume of the solution resulting from the absorption, which is the case in sufficiently high concentrations when the conductivity of the membrane material is itself negligible, the void volume can readily be calculated. The results of these two methods of obtaining the average capillary cross section check quite well. Calculated values of the pore diameters vary directly as the thickness of the membrane, indicating that the effective diameter of the pores is a function not only of their size but also of the length of the path of flow. Bartell (*3*, *4*) has done considerable work on pore dimensions using both Poiseuille's law and Jurin's method (measuring the pressure required to overcome surface tension in the capillaries). With Poiseuille's law he obtained only relative values. Some recent, as yet unpublished, experiments of Bartell using packed carbon and silica membranes show that actual values of the pore dimensions can be obtained by means of Poiseuille's law and that the values agree satisfactorily with values obtained by Jurin's method.

None of these investigators have employed the direct electro-endosmotic method of determining the total effective capillary cross section upon which this investigation is based. Guerout's assumption that the capillaries extend entirely through the membrane would have given accurate results for the pore diameters of transverse wood sections only in the case of infinitesimally thin sections in which none of the tracheids terminate in the section, and the deviations would have increased with an increase in thickness. When the *effective* capillary cross section rather than the *average* is used, no assumption need be made or corrections introduced for type of structure, since the effective capillary cross section itself takes into account the nature of the capillary systems.

APPARATUS AND EXPERIMENTAL PROCEDURE

The apparatus used for the hydrostatic-flow method (fig. 6) is similar in principle to that of Emanueli (*12*) for determining the gas permeability of paper. It consists essentially of a tubular glass vessel divided into three compartments by a wood membrane, M, and a standard capillary tube, C; the former, with rubber gaskets, is clamped between brass flanges and the latter is held by a rubber stopper, R. Mercury manometers, P_1 and P_2, indicate the pressure drops between compartments I and II, and II and III, respectively. A is the intake tube and B is the overflow. After the wood membrane under investigation is fastened in place the apparatus is filled with distilled water through tubes S and S′, care being taken to displace all air from the manometer tubes and connections. A constant

hydrostatic head of water is applied at A, and when the pressure drops through the standard capillary and the membrane come to equilibrium, readings on the manometer tubes are recorded. Reversing the connections so that the hydrostatic head is applied at B on the standard capillary side rather than on the membrane side, with A serving as the overflow, has no effect on the equilibrium pressure-drop ratio.

The effective area of cross section of the wood sections was 2.08 sq. cm. The radii of the several standard capillary tubes used in the experiments ranged from 0.01102 to 0.03681 cm. and the lengths from 15 to 20 cm. The bores of these tubes were determined by the capillary-rise method, employing both benzene and water; tubes showing a maximum bore deviation of more than 0.5 per cent were rejected. The validity of Poiseuille's law for these standard capillaries was then checked by direct trial measurements, using only compartments II and III and applying the hydrostatic pressure at S. The viscosity of the water was determined, with the aid of a temperature-viscosity curve, from the temperature of the efflux water, and the rate of flow from its weight and the time involved.

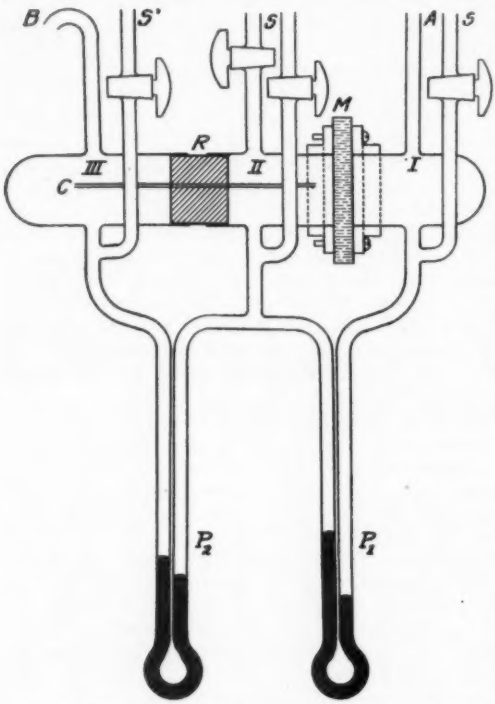

FIG. 6.—Differential pressure-drop apparatus used in obtaining capillary dimensions

CORRECTION FOR TURBULENCE

The calculated and the measured values of V checked in all cases to better than 9 per cent over the range of pressures applied, neglecting any correction for the impact turbulence at the discharge ends of the standard capillary tubes used. The deviation of the observed velocity of flow from the calculated decreased with a decrease in applied pressure. The deviation can be corrected for by using Couette's amplified form of Poiseuille's equation (*24, p. 729*),

$$\eta = \frac{\pi r^4 P}{8Vl} - \frac{1.12dV}{8\pi l} \qquad (11)$$

in which 1.12 is a constant for a submerged capillary and d is the density of the liquid. The ratio of the velocity calculated from this equation to that calculated from the simple equation for different applied pressures is plotted in Figure 7. The average line through these points corresponds quite closely to that through the points representing the ratio of observed rate of flow to that calculated from the simple form of the equation. The lines are approximately straight lines over the range used in the experiments, though they presumably would curve so as to cause a greater and greater deviation from the simple equation at extremely high pressures. Extrapolation of the lines to values of the applied pressure that become infinitesimally small makes the limiting ratio equal to unity, as would theoretically be expected. This graphical method of extrapolation to

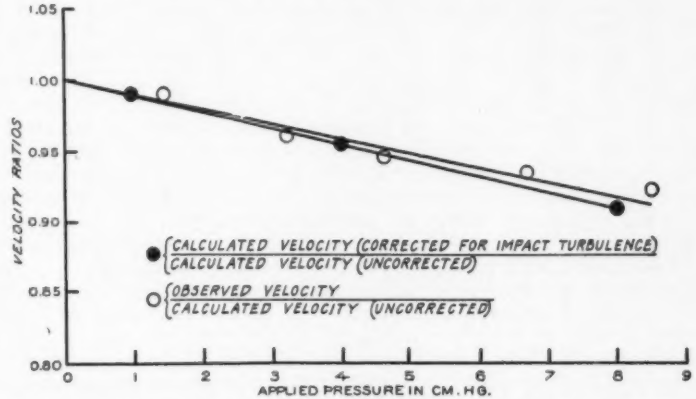

FIG. 7.—Graphical correction for impact turbulence. Capillary dimensions: Radius, 0.03681 cm.; length, 16.02 cm.

determine the limiting ratios has been used as a means of correcting for turbulence throughout this investigation.

Following the measurements made on the wood membranes, employing the differential pressure-drop method, the ratio of the pressure drop along the standard capillary to that across the membrane, $\frac{P_2}{P_1}$, was plotted against the total pressure drop. This ratio decreased with an increase in total pressure. Working with the standard capillary of Figure 7 and with thin transverse membranes, $\frac{P_2}{P_1}$ decreased about 20 per cent while the total applied pressure increased from a few tenths of a centimeter to 5 cm. of mercury. This relationship also was approximately a straight-line relationship, so that extrapolated values could be readily determined. The slope of the line indicates that P_1 increases much more rapidly than P_2 with an increase in total applied pressure—that is, at higher pressures the deviation from Poiseuille's law, presumably caused by such factors as surface friction and internal turbulence in the irregular tracheid passages, combined with the impact turbulence, is greater for the wood membranes than for the standard capillary tube. The

slope of this line varies somewhat with the bore and the length of the standard capillary and with the permeability and the thickness of the wood membranes, but the general nature of the correction was in all cases the same. In all of the calculations to follow the limiting pressure-drop ratios were substituted for the actual experimental values.

MEASUREMENTS

Thin Transverse Sections

Measurements by the differential hydrostatic-flow method were first made on thin transverse sections of different softwoods that were considerably less than a tracheid length in thickness. Table 10 gives the limiting pressure-drop ratios $\frac{P_2}{P_1}$, the effective open capillary cross section q expressed in percentage of the total cross section, obtained from the previous electroendosmosis investigation, and the fourth root of the average fourth power of the lumen diameters of the open tracheids, expressed in μ (in 10^{-4} cm.). This last value should not differ greatly from the average diameter, even though differences of diameter as great as tenfold do exist among tracheids, because it is the mean deviation from the most probable value rather than the maximum deviation that is effective in the measurements. The average lumen diameters obtained from microscopical measurement also appear in Table 10, for comparison with the calculated values. They were obtained by averaging arithmetically the radial and the tangential lumen diameters of several typical radial rows of tracheids extending over an entire annual ring. About 100 lumina were measured on each specimen. The measurements were made with an ocular micrometer, calibrated with a stage micrometer, using thin microtome sections. The values calculated from Poiseuille's law are consistently about 18 per cent lower than the directly observed ones. This is to be expected, since the calculated values are the diameters of the uniform circular capillaries that would give the observed flow, whereas the actual cross sections are by no means circular; in the spring wood they approach square and in the summer wood are rectangular with adjacent sides definitely unequal, to a varying extent.

Variation in the thickness of the sections between the limits given in Table 10 has only a relatively small effect upon the calculated diameters of the capillaries, although the corresponding values of q vary from 77.7 to 28.1 per cent. It is only the open tracheids extending across the entire section thickness that are effective in these experiments; the passage of liquid from tracheid to tracheid through the pits is negligible in comparison, as will be shown later. The diameters obtained with increasing thickness of wood sections thus correspond to a decreasing proportion of the total tracheids. There seems to be a slight tendency for the diameter to decrease with an increase in thickness of the section. This would be expected, since the effective diameter of a capillary of nonuniform bore is determined mainly by the minimum bore, and as the length increases the probability of a smaller bore occurring in the tube will increase, especially as the tracheids taper toward their extremities. This effect is small for these sections, but becomes appreciable for the thicker sections to be considered.

TABLE 10.—*Average lumen diameters determined by the application of Poiseuille's law and by direct measurement*

[Membrane area=2.08 sq. cm.; r_2=0.03681 cm.; l_3=16.02 cm.]

Species of wood; heartwood only	Density of wood	Thickness of wood section l_1	$\frac{P_2}{P_1}$	q (in percentage of total membrane area)	Average diameter of lumen by—	
					Poiseuille's law	Direct measurement
	Gm./c. c.	*Cm.*			μ	μ
Sitka spruce	0.304	0.167	31.0	69.2	22.8	26.3
Do	.304	.173	28.4	68.2	22.3	
Do	.304	.211	24.0	63.4	23.5	
Do	.304	.267	12.7	48.0	22.1	
Alaska cedar	.442	.145	20.7	61.1	18.4	23.1
Do	.442	.175	16.0	58.2	18.2	
Do	.442	.188	14.5	56.7	18.2	
Do	.442	.200	14.0	54.3	18.9	
Western red cedar	.290	.165	29.5	76.7	21.0	27.6
Do	.290	.170	29.0	76.2	21.2	
Do	.290	.190	24.0	75.3	20.5	
Do	.290	.215	21.2	73.5	20.7	
Do	.290	.231	19.8	72.3	20.9	
Do	.290	.236	18.5	71.0	20.6	
Do	.290	.249	17.5	70.0	20.8	
Do	.290	.272	11.6	53.7	20.2	
Do	.290	[a].157	26.7	77.7	19.3	
Do	.290	[a].195	22.0	76.2	19.7	
Do	.290	[b].211	18.0	74.7	18.8	
Do	.290	[b].218	20.0	74.3	20.2	
Douglas fir (Rocky Mountain type)	.526	.130	16.0	55.9	16.1	20.6
Do	.526	.175	15.0	52.0	18.7	
Do	.526	.236	9.0	43.2	18.5	
Western yellow pine	.410	.114	28.5	65.3	18.6	23.0
Do	.410	.157	19.0	61.7	18.3	
Do	.410	.165	20.0	61.2	19.3	
Do	.410	.183	17.0	57.8	19.3	
Do	.410	.244	10.4	44.3	19.9	
Do	.410	.269	5.6	28.1	19.3	

[a] 95 per cent alcohol used instead of water. [b] Benzene used instead of water.

Measurements were made using 95 per cent alcohol and also benzene in place of water to see if a difference in surface wetting or surface viscosity might in any way affect the results. No appreciable effect appeared; the values thus obtained for the diameter of the lumen are very nearly the same as those obtained with water, showing that any differences in specific surface viscosity that may exist are of insufficient magnitude to affect the results. The bulk viscosity of the liquid itself seems to be alone effective.

EFFECT OF APPRECIABLE CHANGES IN THICKNESS

The effect of increasing the thickness of the transverse sections beyond that of a tracheid length was studied. In wood membranes of such thickness a number of tracheid lumina are connected in series through the small openings in the pit membranes, and the question of what capillary dimensions are effective in determining the rate of flow of liquids for such a system thus arises. It is answered by some experiments of Ewart (*13*), who found that under a head of 80 cm. of water 4.0 to 4.2 c. c. of the water flowed per hour through a capillary tube having a radius of 0.0075 cm. and a length of 8 cm.; the theoretical flow for these conditions was 4.3 c. c. per hour. The tube was then cut into 16 lengths of 0.5 cm. and each length was sealed into a tube 0.2 cm. in radius and 5 cm. long. All of these units were

connected in series, thus giving a discontinuous capillary. Under the same head of water 3.8 to 3.9 c. c. passed through the tubes per hour, showing substantially that only the fine capillaries are effective in determining the rate of flow, and that the rate is practically the same as for one capillary with a length equal to the sum of the lengths of the sections, the small variation being accountable for on the basis of increased impact turbulence. When the liquid flows from tracheid to tracheid through the openings in the pit membranes the situation is similar. The size of the openings in the pit membranes should be the determining factor, since the lumen capillaries, relatively speaking, are quite large. The effective length will no longer be the thickness of the sections but the sum of the thicknesses of all the pit membranes traversed in series. Since the thickness of the pit membranes is minute, it can not be determined with any great accuracy. Average values of the thickness of the middle lamella (the cementing layer between adjoining tracheids) were taken as a fairly representative value of the membrane thickness, namely, 0.5 μ (which is 0.5×10^{-4} cm.). It was assumed that the liquid flowed through approximately half the length of a tracheid in flowing from one tracheid to another. According to this, the total membrane thickness x_m cm. traversed by the liquid passing through a transverse section of thickness l and having an average tracheid length t may be approximately expressed by the equation

$$x_m = 0.5 \times 10^{-4}\left(\frac{l}{0.5t} - 1\right) \tag{12}$$

For sections thicker than the maximum tracheid length, equation (10) may be employed in calculating the effective size of the pores in the pit membranes by substituting r_m, the average effective radius of the pores, for r_1, and q_m, the total effective cross section of the pores, for q_1, and also x_m, the total pit membrane thickness, for l_1, thus:

$$r_m = \sqrt{\frac{\pi r^4_2 \, x_m \, P_2}{q_m \, l_2 \, P_1}} \tag{13}$$

If there are any open tracheids extending across the section, the expression becomes more complicated, since flow then takes place both through the pit membranes and the few open tracheids in parallel. Combining the two kinds of capillary structure in parallel with the standard capillary in series, equation (9) becomes

$$\frac{\pi r^4_2 \, P_2}{l_2} = \frac{q_1 \, r^2_1 \, P_1}{l_1} + \frac{q_m \, r^2_m \, P_1}{x_m} \tag{14}$$

where q_1 represents the total effective capillary cross section of the open tracheids and q_m the total effective capillary cross section of the pores in the pit membranes. The value of q secured from the electroendosmosis experiments is equal to the sum of q_1 and q_m. The measured values of q for sections thicker than the maximum tracheid length will be equal to q_m in the case of softwoods free from resin ducts. For the thinner sections q_1 can be obtained with sufficient accuracy by subtracting the minimum value of q (which is q_m) from the value of q for that section.

The Effective Capillary Dimensions of Thick Transverse Sections

Table 11 gives the calculated diameter (fourth root of average fourth power) of pit-membrane pores in wood sections exceeding the maximum tracheid length in thickness, for two softwoods free from resin ducts. The variation in the values is not excessive even when 95 per cent alcohol and benzene are substituted for water, and the values show no regular variation with thickness of the sections. Though the variations in the determined pore diameters do not exceed 50 per cent, the actual pore diameters may vary by 100 per cent or more from the values here obtained because of possible inaccuracy in the assumptions as to path of flow and as to the thickness of the pit membrane; the actual membrane thickness may differ as much as 50 per cent from the value used. The assumption that the liquid on an average flows through half a tracheid length in passing from one tracheid to another may also be in error by 50 per cent. There may in addition be some variation from Poiseuille's law for the system of fine discontinuous capillaries that is not entirely corrected for by the graphical compensation method used. The hydrostatic-flow method, however, seems to give a good approximation of the order of magnitude of the pore diameters, as will be shown in the following part of this paper, in which the pore diameters are determined by two other methods.

Table 11.—*Average diameters of the pores of the pit membranes*

Species of wood	Thickness of section	$x_m \times 10^4$	$\frac{r_1^4}{l_1} \times 10^9$	$\frac{P_3}{P_1}$	q_m (in percentage of total active area of wood section)	Average diameter of pores of pit membranes
	Cm.	*Cm.*				$m\mu$
Alaska cedar	1.218	3.41	1.93	0.0017	0.34	14
Do	.873	2.31	1.93	.0035	.34	17
Do	.582	1.38	1.93	.010	.34	21
Western red cedar	1.090	2.44	.81	.01	.52	15
Do	1.067	2.38	1.99	.0022	.52	11
Do	.795	1.65	1.99	.0045	.52	13
Do	.610	1.15	.81	.024	.52	16
Do	.587	1.08	1.99	.011	.52	16
Do	[a] 1.050	2.33	1.93	.01	.52	23
Do	[a] .678	1.33	1.93	.018	.52	23
Do	[b] .988	2.17	1.93	.005	.52	16
Do	[b] .647	1.25	1.93	.01	.52	17

[a] 95 per cent alcohol used instead of water. [b] Benzene used instead of water.

There may be some deviation from the average diameter (fourth root of the average fourth power) among the pores in the pit membranes; possibly some approach microscopical visibility with a compensating number of minute ones. The order of this deviation will also be shown in the last part of this paper.

The values conform well with the values secured by other investigators for various membranes. Guerout (*19*) obtained 14 to 20 $m\mu$ for the pore diameters of pig bladder, 7 to 17 $m\mu$ for goldbeater's skin, and 21 to 26 $m\mu$ for parchment paper. Duclaux and Errera (*11*) report 26 $m\mu$ for the pore diameter of cellulose acetate membranes.

Hitchcock (*25*) obtained diameters ranging from 5 to 40 $m\mu$ for collodion membranes of different thicknesses. From these values it is seen that the pit membranes have a capillary structure similar in pore dimension magnitudes to those of the natural animal membranes and of the synthetic cellulose derivatives.

The pore sizes obtained appear to be sufficiently large to allow the passage of colloidal solutions containing very fine particles, such as the colloidal carbon that Bailey (*1*, *2*) found to pass through transverse sections of softwoods greater than a tracheid length in thickness. On the whole, however, they are somewhat smaller than the finest structure that can be seen under the highest powered micro-

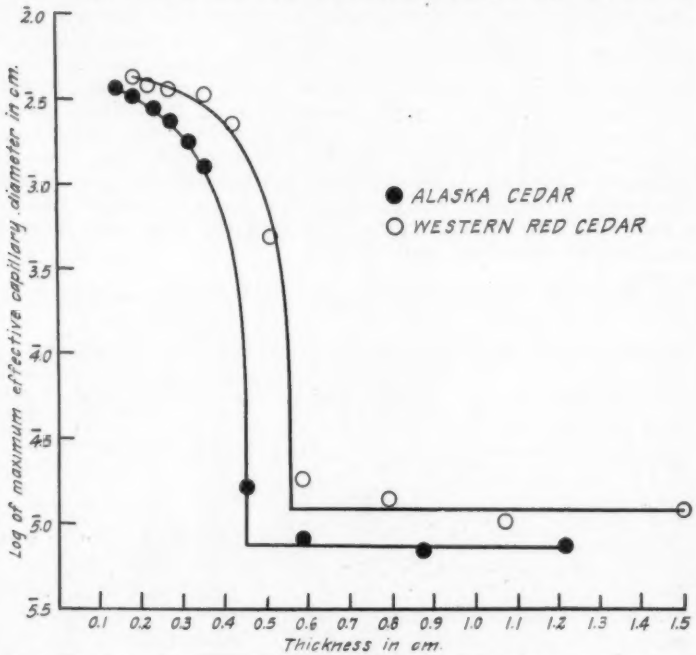

FIG. 8.—Variation of the *average* effective capillary diameter with thickness of transverse sections of heartwood

scope (on an average one-fifth the size of the resolving limit of the microscope). If the presumable checks and pores which Bailey observed in the pit membranes under an exceptionally high magnification are truly effective capillaries, they must represent maximum values under special conditions.

In Figure 8 the logarithms of the effective capillary diameters for different thicknesses of transverse sections of two softwoods free from resin ducts are plotted against the thicknesses of the sections. Up to a section thickness equal to the maximum tracheid length, a critical value, the decreasing diameters represent the effective tracheid-lumen dimensions. In the case of the section thicker than the maximum tracheid length, each diameter represents that of the pores in the pit membranes traversed. The sharp break in the curves

occurs at the maximum tracheid length, the values being practically the same as those obtained in the electroendosmosis investigation. The break is justifiable, though in one case there are no points near it, because of the great effectiveness of the inclusion of only a few tracheids open at both ends and in spite of the fact that the cross section at the tips of each lumen are considerably less than the average. The more gradual transition in the upper part of each curve is due to the fact that an increasing proportion of the open tracheids are cut across near one of their tapering ends as the thickness of the sections increases from nearly a zero value, thus giving an effective diameter which deviates more and more from the average diameter of a tracheid lumen. Using the combined form of the equation for flow through both the open tracheid lumina and the pit membranes in parallel (equation 14), it was found that the pit membrane capillary communication became noticeable only after the proportion of open tracheids was negligible.

LIMITATIONS OF THE HYDROSTATIC-FLOW METHOD

The hydrostatic-flow method of studying the capillary structure of a porous material, combined with the electroendosmotic-flow method, furnishes only average dimensions of the capillary structure. Consequently the diameters of the pores in the pit membranes were determined, in the last part of this investigation, by Jurin's method of finding the air pressure required to just cause the passage of air through wet sections (overcome the surface tension in the fine capillary structure).

SUMMARY OF PART II

A method for determining approximate values of average lumen (cell cavity) diameters and of the diameters of the pores in the pit membranes of softwoods has been developed by combining the data covering the total effective capillary cross sections obtained from electroendosmosis measurements with pressure-permeability measurements and then applying Poiseuille's law.

The calculated effective lumen diameters agree fairly well with the values actually measured.

The calculated pore diameters of the pit membranes are of the same order of magnitude as the pores in some natural animal membranes and in several cellulose derivative membranes. The average value obtained is about a fifth that of the limit of the resolving power of the microscope.

For transverse wood sections thicker than the maximum tracheid (softwood fiber) length the diameter of the average effective continuous capillary passage is determined almost entirely by the diameters of the pit-membrane pores, and does not vary with the thickness of the section. For similar sections thinner than the maximum tracheid length the corresponding capillary diameter increases rapidly with a decrease in the thickness of section because of the inclusion in the effective capillary passage of open tracheid capillaries, which are a thousandfold larger in diameter than the pores in the pit membranes.

The experiments also afford another dynamic physical method of determining the maximum tracheid length. The values thus obtained agree well with the values reported for the electroendosmosis part of this investigation.

III. CAPILLARY STRUCTURE AS INDICATED BY THE OVERCOMING OF CAPILLARITY WITH APPLIED GAS PRESSURE AND BY PERMEABILITY TO COLLOIDAL SOLUTIONS

The determination of the pressure required to overcome the surface tension of liquids in the capillary systems of softwoods—that is, the application of Jurin's law to the softwood membranes used in the preceding parts of the present investigation—permits calculation of the *maximum* effective diameters of the open tracheid lumina in those membranes (for thin sections) and also permits similar calculation of the continuous openings through the pit membranes in the tracheid walls (for thick sections). Further, the permeability of the thick wood membranes to colloidal solutions containing particles of a size both fairly uniform and approximately known supplies a means for determination of the order of magnitude of the active pores in the pit membranes, thus offering verification of the values obtained through Jurin's law and, by comparison with some results of the second part of the investigation, furnishing a basis for estimation of the range in pore sizes.

JURIN'S LAW

Liquids that wet capillary tubes rise in the tubes to a height dependent upon the surface tension of the liquid and the counter pull of gravity on the liquid column. Equilibrium is reached when the resultant force is equal to zero. Therefore,

$$F=\pi r^2 hdg-2\pi r\sigma\cos\theta=0 \tag{15}$$

and

$$\sigma=\frac{rhdg}{2\cos\theta} \tag{16}$$

where σ is the surface tension of the liquid, r the radius of the tube at the meniscus, h the height of rise, d the density of the liquid, g the acceleration of gravity, and θ the angle of contact of the liquid with the capillary surface, all expressed in centimeter-gram-second units. For water and other liquids that wet the capillaries completely, θ is equal to zero and the expression simplifies to

$$\sigma=\frac{rhdg}{2} \tag{17}$$

When σ is known for the liquid used, this equation serves as a means of determining r by merely measuring h. The method, however, can not be used in the case of wood capillaries, because their opacity prevents the measurement of h and also because the irregularity of their capillary systems makes it practically impossible to bring the liquid menisci to the points desired for measurement.

Although the method of equation (17) can not be used for wood capillaries, it is possible to measure the gas pressure required to overcome the capillarity in such systems. The applied pressure that will just cause the removal of the liquid from a single capillary, and thus will barely allow the passage of gas, is the pressure that will overcome the surface tension in the smallest part of the capillary bore. If several capillaries of different bores are combined in a

bundle, the pressure that will just cause the removal of liquid, allowing the passage of gas, will correspond to that required to overcome the surface tension in the tube with the largest minimum bore, which is the same as the maximum effective bore because of the fact that the minimum bore of any irregular capillary tube determines its effectiveness. The water will be displaced first from the tube of least capillary resistance, and the pressure required to do this is the only one that can be directly determined. Thus for the complex capillary systems in wood this method of determining capillary dimensions will always give the largest minimum bore for each of the systems of open capillaries subjected to the gas pressure. The pressure Q (per unit of area) is directly determinable from the equation

$$Q=\frac{2\,\pi\, r\,\sigma\cos\theta}{\pi\, r^2}=\frac{2\,\sigma\cos\theta}{r} \tag{18}$$

or

$$Q=\frac{2\,\sigma}{r}\ (\text{when } \theta=0) \tag{19}$$

For measurements made at 25° C. with water as the liquid to be displaced

$$r=\frac{2\sigma}{Q}=\frac{2\times 72.1}{Q}$$

or

$$r\ (\text{in } \mu)=\frac{1.442}{Q\ (\text{in bars})}=\frac{1.472}{Q\left(\text{in }\frac{\text{kg.}}{\text{cm.}^2}\right)}=\frac{108.3}{Q(\text{in cm. Hg.})} \tag{20}$$

PREVIOUS APPLICATIONS OF JURIN'S LAW

The determination of pore diameters by means of Jurin's law has been studied by Bigelow and Bartell (*3*). Using glass capillaries with diameters ranging from 0.008 to 0.114 cm., they found that the observed and the calculated diameters check quite well, and that the length of the capillaries alone has no effect. Further investigations by Bartell (*3*, *4*) show the effect of the method of preparation of collodion membranes upon the pore diameters obtained by applying Jurin's law. In addition, Bartell and Osterhof (*5*) have recently used this means of determining pore diameters in membranes made up of granular particles of carbon and silica. Their results check quite well with the pore diameters obtained by determining the permeability of the membranes to liquids under hydrostatic pressure, using Poiseuille's law.

APPARATUS

The essential part of the apparatus appears in Figure 9. It consists of a T tube made of brass, with a flange on one arm for clamping wood sections securely over the open end of the arm. The cross section of the tubing terminating in the flange is 0.8 sq. cm.; the applied pressure is operative over this area. The disk plate that holds the wood section in place by means of four screws has in it several small holes distributed over the area of the tube end to allow the free passage of air, while still supporting the membrane enough to prevent rupture from

taking place readily at high pressures. A pure gum rubber gasket clamped between the flange face and the wood section furnishes a seal practically air-tight.

For thin transverse sections of wood, less than a tracheid length in thickness, the gas pressure was obtained from a low-pressure supply of compressed air, and the pressure applied was measured on a mercury or a water manometer; the range employed was from 2 to 20 cm. of mercury. For thicker sections of lower permeability a tank of oxygen under high pressure, having a readily controllable needle valve, formed the source of gas pressure, and the pressure applied was measured by means of a calibrated pressure gauge, which was sensitive to 0.5 kgm. per square centimeter; the range employed was from 1 to 50 kgm. per square centimeter.

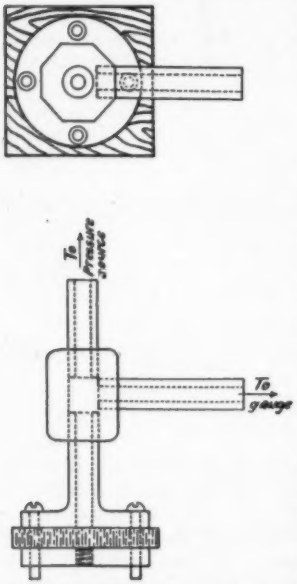

FIG. 9.—Apparatus for overcoming the surface tension of a liquid in the capillary structure of wood

EXPERIMENTAL PROCEDURE

In making the measurements with water a water-soaked section was clamped securely between the flange and its plate, and the apparatus was then dipped into a dish of water just far enough for the liquid barely to touch the bottom of the wood section. The gas pressure was applied gradually, permitting accurate observation of the pressure at which gas bubbles emerged initially from under the immersed plate. By using this technic it was readily possible to distinguish actual passage of gas through the section from the slight gas leak between the nonimmersed flange and the wood; leaks of this nature can not be entirely eliminated at the higher pressures. The possibility of distinguishing the two kinds of gas flow makes this type of flange connection preferable to the cup type.

The rate at which pressure on the wood section is built up has some effect upon the pressure at which gas bubbles appear, an increase in rate causing the pressure to reach a higher value before the bubbles first appear. To prevent the building up of pressure faster than it could be dissipated, in working with the most resistant sections the needle valve controlling the gas was so operated that attaining the final pressure took several minutes. The lag in the dissipation of pressure was not so noticeable with the less resistant sections as with the others. After making a determination the apparatus was disconnected from the pressure line and a drop of water was placed in the tube to assure the resoaking of the upper part of the section; then when the apparatus had stood for a few minutes a check determination was made.

All of the pressure readings presented in this paper are averages of several values. For highly resistant sections, giving pressure readings above 20 kgm. per square centimeter, the values were usually checked to better than 6 per cent and for low-resistance sections to better than 2 per cent. In a few instances a high-resistance section gave a much smaller pressure reading on the second determination than on the first; all readings on such sections were rejected. In each case careful examination of the section showed that rupture had taken place during the first measurement, which usually happened when the pressure was built up too rapidly. Such rupture should be expected at times, since pressures of 50 kgm. per square centimeter are equivalent to the shearing strength of some of the softwoods when green.

Measurements on Thin Transverse Sections

Measurements of the pressures required to overcome the surface tension of water in the open lumen capillaries of the heartwood sections, previously studied, that were less than a tracheid length in thickness are given in Table 12, together with the corresponding calculated lumen diameters. Each diameter represents the largest minimum bore of all the capillaries in the bundle to which the pressure was applied, that is, the maximum effective bore, for the approximately 100,000 tracheids making up the 0.8 sq. cm. cross section. The maximum lumen diameters obtained from the microscopical measurements on matched specimens made for the second part of this paper are also given. In securing the maximum diameters the radial and the tangential lumen diameters for several average radial rows of tracheids extending over an entire annual ring, about 100 lumina on each specimen, were measured. Such maximum diameters naturally are less than those obtained from the statistically large number of lumina that probably are effective in the pressure measurements and that may include abnormal structure not considered in the microscopical measurements; the table shows definitely that they are less.

Resin ducts, extending through the sections, that are largely free from resin and obstructing growths may possibly be effective in the permeability measurements. The two cedars, however, are entirely free from resin ducts, and the small number present in Douglas fir and in Sitka spruce for the specimens studied are of the same order of size as the largest tracheid lumina in those woods. Western yellow pine, therefore, is the only one of the woods considered in which the effect of resin ducts may be appreciable. Since no evident abnormalities are found among the results for the pine, the resin ducts in these specimens also appear to be ineffective.

TABLE 12.—*Maximum effective lumen diameters determined by the application of Jurin's law and by direct measurement*

Species of wood; heartwood only	Thickness of wood section	Pressure required to overcome the surface tension	Maximum effective diameter of lumen by—	
			Jurin's law	Direct measurement
	Cm.	*Cm. of Hg.*	*μ*	*μ*
Sitka spruce	0.172	4.5	48.1	40.8
Do	.198	5.0	43.3	
Do	.262	5.2	41.7	
Do	.317	5.8	37.3	
Alaska cedar	.147	6.1	35.5	32.2
Do	.185	6.5	33.3	
Do	.231	7.8	27.8	
Do	.270	9.3	23.3	
Do	.318	12.6	17.2	
Do	.356	17.3	12.5	
Western red cedar	.182	5.3	40.9	38.0
Do	.218	5.7	38.0	
Do	.269	6.0	36.1	
Do	.355	6.5	33.3	
Do	.420	9.6	22.6	
Douglas fir (Rocky Mountain type)	.183	5.7	38.0	35.0
Do	.198	5.8	37.3	
Do	.274	7.4	29.3	
Western yellow pine	.178	4.1	52.8	43.8
Do	.241	5.1	42.5	
Do	.267	4.8	45.1	

TABLE 13.—*Comparison of pressures required to overcome the surface tension of water and of benzene in the lumen capillaries of white fir heartwood*

Thickness of wood section	Corrected pressure required to overcome the surface tension of water	Maximum effective diameter of lumen	Pressure required to overcome the surface tension of benzene	Pressure required for benzene in terms of that required for water
Cm.	*Cm. of water*	*μ*	*Cm. of water*	*Per cent*
0.211	46.9	62.5	19.0	40.5
.224	47.3	62.0	19.4	41.0
.262	48.0	61.0	19.6	40.8
.282	48.7	60.2	19.8	40.6
.292	48.8	60.0	19.8	40.6
.310	49.6	59.1	20.0	40.3
.373	51.0	57.5	20.9	41.0
Average				40.7

DISPLACEMENT OF BENZENE

It is of interest to determine the pressures required to displace liquids other than water from the capillary structure of wood for the purpose of learning if they wet wood completely. Accordingly, paired thin transverse sections of white fir less than a tracheid length in thickness, of as nearly the same thickness as possible, were oven dried, after which one set was soaked in benzene and the other in water. Measurements were made of the pressure required for gas bubbles barely to pass through the sections. The results are recorded in Table 13. The pressure for each water-soaked section was corrected to agree exactly with the thickness of the corresponding benzene-soaked one, and maximum effective lumen diameters were

then calculated from the corrected values, using equation (20). On the other hand, the complications incident to the swelling of wood in a nonaqueous liquid are far from slight. Although the fact has been established that the swelling of wood caused by water is much greater than that caused by benzene (*22*), and although measurement of these sections showed the average of the radial and the tangential swelling transmitted to the external dimensions of the sections to be 4.9 per cent for water when taking the corresponding dimensions in benzene as standard, yet the information available proved to be insufficient to permit certain calculation of the maximum effective lumen diameters for the benzene-soaked sections. Under the circumstances the angle of contact between benzene and wood can not be calculated positively. A calculation based partly on some assumptions, however, indicates that the angle at most is not large and that it may be zero; if it is zero, benzene wets wood completely. Table 13 presents the experimental results.

Measurements on Thick Transverse Sections

Measurements were also made on transverse sections of wood thicker than the maximum tracheid length. In this case the pressure required to just displace the water from the irregular systems of tracheid lumina and pit-membrane pores is that required to overcome the surface tension in the smallest part of the bore of the most effective combination of pores in series. Table 14 gives the results of these measurements and the calculated *maximum* effective pore diameters of the pit membranes; these values are four to eight times as great as the corresponding *average* values obtained in the hydrostatic-flow study. Such differences in order of magnitude should be expected, since the pores are most probably not all of the same size. The maximum effective values thus serve as a check upon the validity of the order of the average pit-membrane pore diameters obtained by the hydrostatic-flow method.

Table 14.—*Maximum effective diameters of the pores of pit membranes, determined by the application of Jurin's law*

Species of wood; heartwood only	Thickness of wood section	Pressure required to overcome the surface tension	Maximum effective diameter of the pores of pit membranes
	Cm.	*Kg./sq. cm.*	*mμ*
Sitka spruce	1.103	30	98
Do	.828	18	164
Do	.574	21	140
Do	.538	18	164
Alaska cedar	1.218	40	74
Do	.873	43	68
Do	.582	37	80
Do	.450	18	164
Western red cedar	1.500	24	123
Do	1.067	28	105
Do	.795	21	140
Do	.587	16	184
Douglas fir (Rocky Mountain type)	1.310	43	68
Do	.735	28	105
Do	.520	24	123
Western yellow pine	1.370	18	164
Do	.835	16	184

There seems to be a slight tendency for the maximum effective pore diameters to decrease slightly with an increase in thickness of the wood sections. Such decrease may be readily explained by means of the fact that the greater the number of pits traversed in series the less likely it is that any one path through the section will have all large pore openings; the smallest of all of the maximum pores traversed in series is the controlling one.

Figure 10 shows the variation in the *maximum* effective capillary diameters, expressed as the logarithms of the dimensions in centimeters, for a large range of thicknesses of transverse sections of two softwoods free from resin ducts. The curves are almost identical in shape with the similar curves for *average* effective diameters given earlier in this paper. A break occurs at the maximum tracheid length, since the change in effective pore diameters for sections thicker than this length is slight, whereas the increase in capillary diameters for decreasing thicknesses is very rapid below the maximum tracheid length because of the inclusion of open tracheids in the active capillary system.

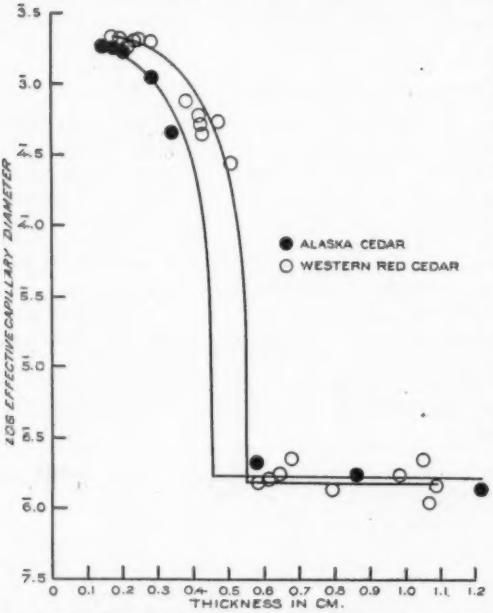

FIG. 10.—Variation of the *maximum* effective capillary diameter with thickness of transverse sections of heartwood

The curvature at the upper ends of these graphs is due to the fact than an increasing proportion of the open tracheids are cut across near one of their tapering ends as the thickness of the sections increases from nearly a zero value, thus giving an effective diameter which deviates more and more from the average diameter of a tracheid lumen, in the same manner as that of the *average* effective diameter curves just cited.

Determining the thickness at which the break in the curves of Figure 10 occurs furnishes a third independent method of securing the maximum tracheid length. Values for the maximum tracheid length obtained by all of these methods, together with the values obtained by direct measurement as made or compiled by the United States Forest Products Laboratory, are given in Table 15. The agreement is satisfactory, especially when the fact that the direct-measurement values were obtained on entirely different specimens is considered.

TABLE 15.—*Maximum tracheid lengths obtained by four independent methods*

Species of wood	Maximum tracheid length by—				
	Direct microscopical measurement		Electro-endosmotic flow	Hydrostatic flow	Overcoming surface tension
	Number of specimens	Value			
		Cm.	*Cm.*	*Cm.*	*Cm.*
Sitka spruce	200	0.49	0.52	----------	0.53
Alaska cedar	----------	----------	.47	0.45	.45
Western red cedar	----------	.45	.54	.55	.56
Douglas fir (Rocky Mountain type)	4,550	.76	.50	----------	.49
Western yellow pine	100	.40	.57	----------	.55

SECTIONS CUT IN EACH OF THE THREE STRUCTURAL DIRECTIONS

Table 16 assembles the maximum effective capillary diameters, determined by means of Jurin's law, for wood sections cut in each of the three different structural directions. The values for the transverse sections are averages of the values, given in Table 14, for sections exceeding in thickness the maximum tracheid length. The values for the radial and the tangential sections are for those 0.06 to 0.2 cm. thick (17 to 50 tracheid widths in thickness). The pore diameters for the radial sections, through which the passage of gas is in a tangential direction, are in all cases somewhat smaller than for the corresponding transverse sections. The displacement of water by gas through these two kinds of sections is very likely through exactly the same structure, the difference being due mainly to the fact that ten to twenty times as many pit membranes are traversed in series in passing through the radial sections as in passing through the transverse ones. Traversing a number of pit membranes in series gives the minimum value for the diameters of the maximum pit-membrane pores, whereas traversing only one or two membranes in series is likely to give a single maximum value, one probably greater than the minimum for several such pores.

TABLE 16.—*Maximum effective capillary diameters of sections cut in each of the three structural directions, as determined by the application of Jurin's law*

[Thickness of sections: Transverse, 1 to 4 tracheid lengths; radial and tangential, 0.06 to 0.2 cm. (17 to 50 tracheid widths)]

Species of wood; heartwood only	Maximum effective capillary diameters					
	Transverse sections		Radial sections		Tangential sections	
	Number of specimens	Value	Number of specimens	Value	Number of specimens	Value
		mμ		*mμ*		*mμ*
Sitka spruce	4	141	4	80	3	111
Alaska cedar	3	74	9	63	8	103
Western red cedar	4	138	7	93	5	131
Douglas fir (Rocky Mountain type)	3	99	----------	----------	2	103
Western yellow pine	2	174	5	76	6	152

In the species containing them the resin ducts, the effective diameters of which in these specimens are still somewhat larger than pore size even though they presumably approach it because of partial clogging, may in part account for the differences between the observed pore diameters for transverse and for radial sections.

The pore-diameter values are somewhat larger for the tangential wood sections, where the displacement of water by gas is in a radial direction, than for the radial ones. This increase is probably due to the ray cells, and in some cases to radial resin ducts. The end walls of the individual ray cells may contain pores larger than those of the pit membranes. The results show, however, that in none of the specimens investigated are the ray cells completely open through the section. This circumstance is to be expected, since the thinnest sections are three ray-cell lengths in thickness. The end walls of the ray cells must nevertheless include a very large percentage of voids; such a condition is indicated in the first part of this paper by the fact that the electroendosmotically determined effective cross section of the tangential sections approaches quite closely the microscopically determined void cross section of the rays.

PERMEABILITY OF WOOD TO COLLOIDAL SOLUTIONS

The permeability of softwood to colloidal solutions containing particles of approximately known size was tested as a check upon the calculated capillary dimensions. A mercury sol of 0.02 gm. per liter, prepared by the Bredig electrical condensation method with potassium citrate (0.0025 normal) as stabilizing agent, was used.[7] The average size, 8 $m\mu$, of the particles of this sol, which were quite uniform, was obtained by the method of fluctuations developed by Smoluchowski (*37*). Nephelometric analysis showed no change in the concentration of the sol when wood sawdust was added. The fact that the sol is not perceptibly coagulated by wood should be expected, since both are electronegative with respect to water. A ferric-oxide sol, which is electropositive with respect to water, was coagulated by wood and hence could not be used.

The passage of the mercury sol through the thick transverse sections of Sitka spruce, Alaska cedar, western red cedar, and Douglas fir was tested, using the apparatus of Figure 9. Ten cubic centimeters of the sol was placed in the tube above the membrane and a pressure of one-half atmosphere was applied. In one case 9.8 c. c. of the sol passed through a section in 18 hours, with a reduction in concentration to about one-tenth its original value. This, as well as other experiments that gave similar results, shows that the sections, although somewhat permeable, also act as partial ultrafilters. Owing to the electrical repulsion between the mercury particles and the wood surface, both of which are negatively charged, it is necessary for the capillary openings to be somewhat larger than the colloidal particles in order for the latter to pass through freely. For such small dimensions the openings may in fact have to be several times the diameter of the particles. The average pore diameters previously obtained range from 12 to 20 $m\mu$. Openings of such size in a charged wall may readily hold back similarly charged particles 8 $m\mu$ in diameter.

[7] This sol was obtained from F. W. Laird, of the chemistry department of the University of Wisconsin. He also determined the particle size.

The maximum pore diameters reported in this paper, which are four to eight times as large as the average values, can, however, hardly be expected to be impervious to the mercury sol. The fact that partial filtration is obtained, therefore, furnishes a check upon the order of magnitude of the pore diameters obtained by the two preceding methods.

A further check upon the partial filtration effect was obtained by placing some of the sol in the tube above the wood section (fig. 9) and applying a pressure of the order of that required to blow gas through the wet sections. An Alaska cedar water-soaked section that had previously required a pressure of 41 kgm. per square centimeter to displace the water and allow the passage of gas required 42 kgm. pressure for gas bubbles to appear after a little of the sol was placed in the tube. The resulting opacity of the water into which the section dipped indicated the passage of sol. The experiment was repeated several times; each time a greater pressure was required for the gas to pass, and each time the concentration of mercury particles passing through decreased. Finally, no gas would pass through the section below a pressure of 52 kgm. per square centimeter, at which value the section broke. Practically no mercury particles passed through the section on the last application of pressure. Similar results were obtained with other sections. Substituting india ink for the mercury sol also gave similar results, except perhaps for the fact that the sections were slightly more permeable to it than to the mercury sol. These experiments thus show that part of the continuous longitudinal capillary structure of softwoods is sufficiently coarse to allow the passage of colloidal mercury solutions and of india ink, but nevertheless part of the structure is sufficiently fine to serve as a partial ultrafilter. Continued pressure filtration, however, will eventually cause clogging of even the larger capillaries, so that the section finally becomes practically impervious.

The fact that some india ink can be forced through the continuous longitudinal structure of softwoods is a confirmation of the results obtained by Bailey (*1*).

SUMMARY OF PART III

The maximum effective lumen diameters and the maximum effective pore diameters of the pit membranes of the heartwood of several softwoods have been determined by the overcoming of the surface tension of liquids in the capillary structure.

The maximum effective lumen diameters agree well with the values obtained by actual measurement.

The calculated maximum pore diameters of the pit membranes are four to eight times as large as the average values obtained by the hydrostatic-flow method.

Maximum tracheid lengths obtained from the data of this part of the investigation agree satisfactorily with values obtained by electro-endosmotic-flow studies and by hydrostatic-flow studies, as well as with those obtained by actual measurement.

The permeability of the wood sections to colloidal solutions of mercury and of india ink serves as a check upon the order of the sizes of the pores making up the pit membranes.

GENERAL CONCLUSIONS

The investigation reported here, in which four different dynamic physical methods of studying the structure of wood have been developed and applied, shows definitely that considerable information on the structure of wood can be obtained by means other than microscopical. Moreover, the dynamic physical methods here developed can be extended to the study of structure below the range of microscopical visibility. The justification for the use of these physical methods, each of which is known to be valid for coarser structure, has been established sufficiently by the fact that the independent methods have given consistent results. For example, the *average* effective continuous capillary diameters for longitudinal flow, obtained by combining the electroendosmosis data for the total capillary cross section with the pressure-permeability data and applying Poiseuille's law, as would be expected, are slightly smaller than those for the *maximum* effective continuous capillary diameters obtained by overcoming the surface tension in the wood capillaries. The two methods are entirely independent; although each measures slightly different structure, nevertheless the results present only the type of variations that should be expected. The first method depends upon the assumption that the passage of liquid from tracheid to tracheid in thick sections of softwood is primarily through an effective capillary length equal to that of the combined pit-membrane thicknesses traversed in series; the second involves no such assumption. The results thus tend to show also that the major part of the flow from tracheid to tracheid is through the pits; microscopical examination has suggested this, but has never proved it conclusively. Accordingly, it is justifiable to assume that the fine capillaries carrying the direct intertracheid flow are those in the pit membranes.

The physical methods developed, besides having the decided advantage of extending the study of capillary dimensions below those of microscopical visibility, have the further advantage of giving results more of a statistical nature than ordinary microscopical examination would give. For example, the measurement of the maximum, minimum, and average tracheid lengths by the electroendosmotic means is automatically obtained in a statistical form for about 1,000,000 tracheids. The other two dynamic methods of obtaining the maximum tracheid length, namely, by hydrostatic-flow studies and by overcoming the surface tension in the capillaries, likewise include a similarly large number of tracheids. In addition, the results of these three statistical methods of obtaining the maximum tracheid length agree satisfactorily.

The major part of this investigation has been devoted to a development of methods. From further work now in progress data are being obtained for different species, heartwood is being compared with sapwood, and green wood with resoaked seasoned wood. These data will help in characterizing the capillary structure of wood and in explaining the complex pit mechanism.

GENERAL SUMMARY

Practically all of the available information on the structure of wood has been obtained by microscopical examination. Unfortunately, such studies have at least two major limitations. The first one is

the limit of the resolving power of the microscope, which makes it impossible to observe structure finer than 0.1 μ and to obtain any detailed information on even coarser structure. For this reason very little is known about the pit mechanism, the thinned portions of the cell wall that serve as a means of communication from lumen to lumen. The capillary nature of the pit membranes remains quite unknown, although it has been shown in a qualitative way for seasoned wood that there is a continuous capillary communication from lumen to lumen through the pits even for colloidal india ink.

The second limitation of microscopical studies of wood structure is the difficulty involved in collecting statistical data on average dimensions of the various structural elements, such as tracheid lengths and lumen diameters. An exceedingly large number of measurements have to be made in such cases in order to obtain fair averages. The time consumed in a study of this nature has greatly limited the amount of such information available.

Because of the limitations of microscopical methods the dynamic physical methods considered in this paper were developed and applied. Four distinct methods of study have been used; the results obtained through them may be summarized as follows:

Electroendosmotic flow.—The total effective capillary cross sections of several different softwood sections cut in each of the three structural directions were determined by means of electroendosmotic-flow studies. From the change in rate of electroendosmotic flow with changes in the thickness of transverse sections the maximum, minimum, and average tracheid lengths were determined, as well as the effective continuous pit-communication cross section.

Hydrostatic flow.—Combining the electroendosmotic-flow data with those obtained from hydrostatic-flow studies, the average effective lumen diameters and the average effective pit-membrane pore diameters were determined. The former agree with values obtained by microscopical measurement. The latter are of the same order of magnitude as the pores in other natural and artificial membranes. Maximum tracheid lengths obtained from the hydrostatic studies agree with the values obtained by the electroendosmotic method.

Overcoming surface tension of water in the capillary structure.—With the surface-tension method of investigation the maximum effective lumen diameters and maximum effective pit-membrane pore diameters were determined. The former agree with values obtained microscopically. The latter are four to eight times as large as the average effective values obtained by the other methods. This physical method, which furnishes a third independent dynamic means of determining the maximum tracheid length, gives values that agree with the other values.

Permeability to colloidal solutions.—Though the wood sections studied are somewhat permeable to colloidal mercury and to india-ink sols, they also act as partial ultrafilters. This fact should be expected, since the mercury particles, although about a tenth as large as the largest pit-membrane pores, are of the same order of size as the average effective pit-membrane pore diameters.

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LITERATURE CITED

(1) BAILEY, I. W.
1913. THE PRESERVATIVE TREATMENT OF WOOD. II. THE STRUCTURE OF THE PIT MEMBRANES IN THE TRACHEIDS OF CONIFERS AND THEIR RELATION TO THE PENETRATION OF GASES, LIQUIDS, AND FINELY DIVIDED SOLIDS INTO GREEN AND SEASONED WOOD. Forestry Quart. 11: [12]–20, illus.

(2) ———
1915. THE EFFECT OF THE STRUCTURE OF WOOD UPON ITS PERMEABILITY. NO. I—THE TRACHEIDS OF CONIFEROUS TIMBERS. Amer. Ry. Engin. Assoc. Proc. 16: 835–853, illus.

(3) BARTELL, F. E.
1912. PORE DIAMETERS OF OSMOTIC MEMBRANES. Jour. Phys. Chem. 16: [318]–335, illus.

(4) ——— and CARPENTER, D. C.
1923. THE ANOMALOUS OSMOSE OF SOLUTIONS OF ELECTROLYTES WITH COLLODION MEMBRANES. II. THE EFFECT OF PORE DIAMETER. Jour. Phys. Chem. 27: [252]–269, illus.

(5) ——— and OSTERHOF, H. J.
1927. THE WORK OF ADHESION BETWEEN SOLID AND LIQUID PHASES. Ztschr. Phys. Chem. 130: 715–723, illus.

(6) BETHE, A., and TOROPOFF, T.
1915. ÜBER ELEKTROLYTISCHE VORGÄNGE AN DIAPHRAGMEN. TEIL II. Ztschr. Phys. Chem. 89: 597–637, illus.

(7) BIGELOW, S. L.
1907. THE PERMEABILITIES OF COLLODION, GOLD BEATER'S SKIN, PARCHMENT PAPER AND PORCELAIN MEMBRANES. Jour. Amer. Chem. Soc. 29: 1675–1692, illus.

(8) ——— and BARTELL, F. E.
1909. THE SIZE OF THE PORES IN PORCELAIN, AND OSMOTIC EFFECTS. Jour. Amer. Chem. Soc. 31: 1194–1199, illus.

(9) BRIGGS, T. R., BENNETT, H. S., and PIERSON, H. L.
1918. ELECTRICAL ENDOSMOSE. II. Jour. Phys. Chem. 22: [256]–272, illus.

(10) BURTON, E. F.
1906. ON THE PROPERTIES OF ELECTRICALLY PREPARED COLLOIDAL SOLUTIONS. Phil. Mag. and Jour. Sci. (6) 11: [425]–447, illus.

(11) DUCLAUX, J., and ERRERA, J.
1924–25. LE MÉCANISME DE L'ULTRA-FILTRATION. Rev. Gén. Colloïdes 2: 130–139, 1924; 3: [97]–103, 1925.

(12) EMANUELI, L.
1927. THE EMANUELI POROSITY TESTER. Paper Trade Jour. 85 (10): 48–50, illus.

(13) EWART, A. J.
1905. THE ASCENT OF WATER IN TREES. Roy. Soc. [London], Phil. Trans. (B) 198: 41–85, illus.

(14) FAIRBROTHER, F., and MASTIN, H.
1924. STUDIES IN ELECTRO-ENDOSMOSIS. PART I. Jour. Chem. Soc. [London] 125: 2319–2330, illus.

(15) FREUNDLICH, H.
1925. ON THE ELECTROKINETIC POTENTIAL. Colloid Symposium Monograph 3: 7–16, illus. New York, The Chemical Catalog Company (Inc.).

(16) ———
[1926.] COLLOID AND CAPILLARY CHEMISTRY. Translated from German ed. 3 by H. S. Hatfield. 883 p., illus. London.

(17) GRIFFIN, G. J.
1919. BORDERED PITS IN DOUGLAS FIR: A STUDY OF THE POSITION OF THE TORUS IN MOUNTAIN AND LOWLAND SPECIMENS IN RELATION TO CREOSOTE PENETRATION. Jour. Forestry 17: 813–822, illus.

(18) ———
1924. FURTHER NOTE ON THE POSITION OF THE TORI IN BORDERED PITS IN RELATION TO PENETRATION OF PRESERVATIVES. Jour. Forestry 22 (6): 82–83.

(19) GUEROUT, A.
1872. SUR LES DIMENSIONS DES INTERVALLES POREUX DES MEMBRANES. Compt. Rend. Acad. Sci. [Paris] 75: 1809–1812.

(20) HARRISON, W.
1911. THE ELECTRICAL THEORY OF DYEING. Jour. Soc. Dyers and Colourists 27: 279–290, illus.
(21) ———
1921. ELECTRICAL THEORY OF ADSORPTION. Faraday Soc. Trans. 16 (app.): 116–118. (Separately paged.)
(22) HASSELBLATT, M.
1926. DER WASSERDAMPFDRUCK UND DIE ELEKTRISCHE LEITFÄHIGKEIT DES HOLZES IN ABHÄNGIGKEIT VON SEINEM WASSERGEHALT. Ztschr. Anorgan. u. Allg. Chem. 154: 375–385, illus.
(23) HELMHOLTZ, H.
1879. STUDIEN ÜBER ELECTRISCHE GRENZSCHICHTEN. Ann. Phys. u. Chem. (n. F.) 7: [337]–382.
(24) HERSCHEL, W. H.
1926. CONSISTENCY. *In* Alexander, J., ed., Colloid Chemistry, Theoretical and Applied 1: 727–737. New York, The Chemical Catalog Company (Inc.).
(25) HITCHCOCK, D. I.
1926. THE SIZE OF PORES IN COLLODION MEMBRANES. Jour. Gen. Physiol. 9: 755–762, illus.
(26) MCBAIN, J. W.
1921. [ELECTRICAL ENDOSMOSIS.] Faraday Soc. Trans. 16 (app.): [150]. (Separately paged.)
(27) REYNOLDS, O.
1883. AN EXPERIMENTAL INVESTIGATION OF THE CIRCUMSTANCES WHICH DETERMINE WHETHER THE MOTION OF WATER SHALL BE DIRECT OR SINUOUS, AND OF THE LAW OF RESISTANCE IN PARALLEL CHANNELS. Roy. Soc. [London], Phil. Trans. 174: 935–982, illus.
(28) SAXÉN, U.
1892. UEBER DIE RECIPROCITÄT DER ELECTRISCHEN ENDOSMOSE UND DER STRÖMUNGSSTRÖME. Ann. Phys. u. Chem. (n. F.) 47: [46]–68.
(29) SCARTH, G. W.
1928. THE STRUCTURE OF WOOD AND ITS PENETRABILITY. Paper Trade Jour. 86 (17): 53–58, illus.
(30) STAMM, A. J.
1926. ELECTROENDOSMOSE THROUGH WOOD MEMBRANES. Colloid Symposium Monograph 4: 246–257, illus. New York, The Chemical Catalog Company (Inc.).
(31) ———
1927. THE ELECTRICAL RESISTANCE OF WOOD AS A MEASURE OF ITS MOISTURE CONTENT. Indus. and Engin. Chem. 19: 1021–1025, illus.
(32) ———
1928. EFFECT OF ELECTROLYTES ON ELECTROENDOSMOSE THROUGH WOOD MEMBRANES. Colloid Symposium Monograph 5: 361–368, illus. New York, The Chemical Catalog Company (Inc.).
(33) ———
1928. THE STRUCTURE OF SOFTWOODS AS REVEALED BY DYNAMIC PHYSICAL METHODS. Colloid Symposium Monograph 6: 83–108, illus. New York, The Chemical Catalog Company (Inc.).
(34) STOCK, J.
1912. ÜBER OBERFLÄCHENLEITUNG UND DICKE ELEKTRISCHER DOPPELSCHICHTEN. Anz. Akad. Wiss. Krakau, Math. Naturw. Kl. (A) 1912: [635]–656, illus.
(35) STRICKLER, A., and MATHEWS, J. H.
1922. STUDIES IN ELECTRIC-ENDOSMOSE. Jour. Amer. Chem. Soc. 44: 1647–1662, illus.
(36) SUDWORTH, G. B.
[1927.] CHECK LIST OF THE FOREST TREES OF THE UNITED STATES, THEIR NAMES AND RANGES. U. S. Dept. Agr. Misc. Circ. 92, 295 p.
(37) SVEDBERG, T.
1924. COLLOID CHEMISTRY; WISCONSIN LECTURES. 265 p., illus. New York, The Chemical Catalog Company (Inc.).

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